Crossosoma

Southern California Botanists, Inc.
— Founded 1927 —

Views published in *CROSSOSOMA* are those of the contributing author(s) and are not necessarily those of the editors, the membership of Southern California Botanists Inc., or the SCB Board of Directors, unless explicitly stated.

CONTENTS

Cover: Eriastrum densifolium, photographed by Sarah De Groot

PRELIMINARY MORPHOMETRIC ANALYSIS OF *ERIASTRUM DENSIFOLIUM* (POLEMONIACEAE) POPULATIONS FROM LYTLE CREEK AND LA CADENA AVENUE, SANTA ANA RIVER WATERSHED

Sarah J. De Groot

Rancho Santa Ana Botanic Garden and Claremont Graduate University
1500 N. College Ave.
Claremont, CA 91711
sarah.degroot@cgu.edu

ABSTRACT: Plants of *E. densifolium* growing at Lytle Creek and the La Cadena Avenue crossing of the Santa Ana River have been suggested to be hybrids involving *E. densifolium* subsp. *sanctorum*, a federally endangered subspecies. Using multivariate analysis of morphological characters, relative warp analysis, and elliptic Fourier functions, these two populations were found to be morphologically intermediate between subsp. *sanctorum* and a group containing samples of subspp. *elongatum* and *austromontanum*. These results could be explained by a hybrid origin of each population, or the populations may be simply intermediate forms. *E. densifolium* is a highly variable species that appears to be composed of a number of ecological races, which are not well characterized and warrant further study.

KEYWORDS: *Eriastrum densifolium, E. densifolium* subsp. *sanctorum*, hybrid, intermediate, La Cadena Avenue, Lytle Creek, morphology, Santa Ana River

INTRODUCTION

Gilia densifolia subsp. *sanctora* was first described by Milliken in 1904 (p. 39), and later transferred to *Eriastrum densifolium* by Mason (1945: 75). It was distinguished from typical *E. densifolium* by the size of the corolla, "…fourteen to fifteen lines long [about 30 mm] and proportionately ample" (Milliken 1904: 39; type specimen [UC 52454] has corollas >25 mm). These characters seem to hold fairly well, because subsp. *sanctorum* generally has been recognized as distinct from other subspecies by the vast majority of authors who have treated it (e.g., Craig 1934; Jepson 1943; Mason 1945; Harrison 1972). Plants usually occur on higher floodplains above washes, in sandy alluvial soils (Zembal and Kramer 1984).

The only range or locality information listed in the protologue was "Santa Ana River near Riverside…" However, from field notes and herbarium specimens, it is apparent that the type collection was made at the Spanishtown Crossing of the Santa Ana River, which today is where Riverside Ave./Main St. crosses the river. Plants of subsp. *sanctorum* occurred from the foot of the San Bernardino Mountains all the way down into Orange County. For example, J.T. Howell 2985, collected in Santa Ana Canyon in 1927 (RSA), has corollas 27-29.5 mm long, and was cited by Craig (1934: 390) as typical *sanctorum*.

More recent surveys and collections have shown that the present distribution of this subspecies has become restricted to the upper portions of the Santa Ana River drainage in the San Bernardino Valley, namely, the area near Highland, Mentone, and Redlands in San Bernardino County, California (Zembal and Kramer 1984; California Natural Diversity Database [CNDDB]). A few plants have been reported near Colton and Riverside (CNDDB), and although plants had been collected in the Santa Ana River

Canyon in Orange County, all Orange County populations by now are probably extirpated (Zembal and Kramer 1984; Marsh 1988). Outside of the Santa Ana River bed, plants have been reported from Plunge Creek, Cajon Wash, Lytle Creek, and several other localities (CNDDB; Zembal and Kramer 1984). A shrinking range and loss of suitable habitat were reasons cited for its listing as endangered by the federal government (Kramer 1987).

Almost since the time they were first collected, the plants at Lytle Creek have been suspected hybrids. Craig (1934) cited them as intermediate between subsp. *sanctorum* and subsp. *elongatum*. Subsequent authors have reiterated this (Wheeler 1988; Burk et al. 1989). However, little quantitative study has been done involving these plants. The U.S. Fish and Wildlife Service continues to recognize them as the endangered subsp. *sanctorum*. At another site of purported hybrids along Cajon Wash, a number of corollas were measured and many were found to be intermediate in length between subsp. *sanctorum* and subsp. *elongatum* (La Pré and Pendleton 1988). More recently, plants found near the La Cadena Avenue crossing of the Santa Ana River also appeared to be intermediates between subsp. *sanctorum* and possibly subsp. *austromontanum*.

Although five subspecies of *E. densifolium* have been recognized by most taxonomists (e.g., Craig 1934; Mason 1945; Harrison 1972), the species is remarkably variable and some authors have found it difficult to define precisely the circumscriptions of the subspecies (e.g. Craig 1934; Brunell and Whitkus 1997, 1999a, 1999b). Identification also has been problematic. For example, the RSA herbarium has two sheets of Swinney 2294, one identified as subsp. *elongatum*, and the other identified as *austromontanum* (det. by O. Mistretta, Oct. 2005). It does not appear to be a mixed collection. A sampling of the morphological diversity in corolla shape and size is illustrated in Figures 1-5, and some leaves are shown later in the paper, in Figure 8.

Geometric morphometric data has been used successfully to distinguish plant species or hybrid populations (Premoli1996; Olsson et al. 2000; Dickinson et al. 1987; Shipunov and Bateman 2005). McLellan and Endler (1998) classified leaves based on landmarks and elliptic Fourier functions. In a study of two species of *Acer* and their hybrid, Jensen et al. (2002) used traditional measurements, elliptic Fourier coefficients, and relative warp scores to demonstrate that the hybrids were morphologically intermediate between the parent species. Thus, quantitative morphological data can be informative in studies of potential hybrid populations.

This paper reports preliminary findings of a morphometric study involving the Lytle Creek population, the La Cadena Avenue population, and a population each of subsp. *sanctorum*, subsp. *elongatum*, and subsp. *austromontanum*, for reference. The main goal was to see how each intermediate population was related to each of the three subspecies and, in particular, to the endangered subsp. *sanctorum*.

METHODS

Fifteen flowering individuals per population were selected arbitrarily and sampled from one population each of *E. densifolium* subsp. *sanctorum*, subsp. *elongatum*, and subsp. *austromontanum*, along with two intermediate populations: one at Lytle Creek just south of Interstate 210, and one at the La Cadena Avenue crossing of the Santa Ana River (Table 1; Figure 6). Populations of the subspecies were chosen based on their resemblance to type material and proximity to type localities.
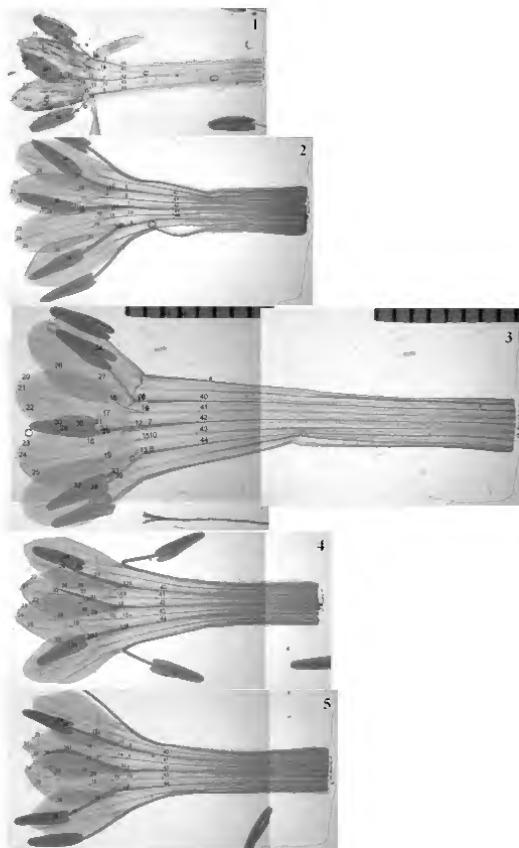
Figures 1-5 (top to bottom). Sample dissected corollas of *Eriastrum densifolium* subspecies, with landmarks used in this analysis.
1. Subsp. *austromontanum* (Mormon Rocks).
2. Subsp. *elongatum* (Vineyard Cyn B).
3. Subsp. *sanctorum* (Alabama St).
4. Intermediate from Lytle Creek.
5. Intermediate from La Cadena Ave. Scale (in mm) is the same for all photos.

Table 1. Summary of localities sampled.

Subspecies	Population Name	County (California)	Latitude N	Longitude W	Elevation (m)
sanctorum	Alabama Street	San Bernardino	34.09694	117.20972	347
elongatum	Vineyard Cyn B	Monterey	35.83702	120.62572	336
austromontanum	Mormon Rocks	San Bernardino	34.31639	117.49333	988
intermediate	La Cadena	San Bernardino	34.04590	117.32332	889
intermediate	Lytle Creek	San Bernardino	34.13264	117.35462	1284

An open corolla from each of fifteen individuals per population was chosen arbitrarily. It was dissected open by removing the petal to the lower left (when the flower was viewed from the front), and photographed along with a metric rule at 10x through an Olympus SZH stereo microscope, using a SPOT RT Color 2.2.1 digital camera and SPOT software (version 4.1.1, © 1997-2004 Diagnostic Instruments, Inc.). Forty-four landmarks and semi-landmarks were placed on the same two petals and three stamens in each image (those in the center after the removal of one petal), with TpsDIG (1.40, Rohlf 2004). Landmarks were placed at presumably homologous points, such as bi- or trifurcations of
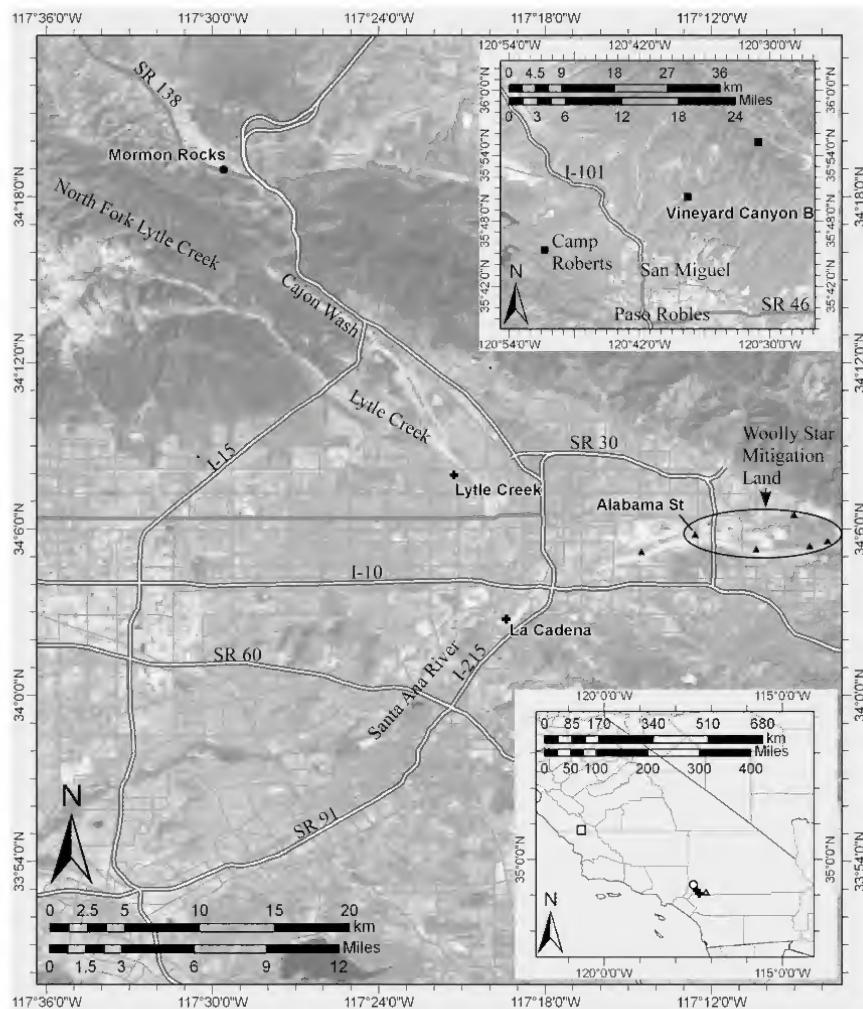
Figure 6. Map of *Eriastrum densifolium* sites sampled in this study. Main map shows the upper Santa Ana River drainage area, mitigation land and sites sampled in this study. Top inset shows the location of the Vineyard Canyon B (*elongatum*) population. Bottom inset shows the general location of the five populations in southern California (created with ArcMap® 9.1).

veins, anastomoses, sinuses, filament divergence points, and where veins met the margins of the corolla. Semi-landmarks were placed along the veins or margins of the corolla, to capture more general aspects of the form (Figure 7). Landmarks were rescaled from pixels to millimeters in CoordGen6 (part of the Integrated Morphometrics Package [IMP], Sheets 2002), and saved in X1Y1…CS format. A matrix of 95 measurements in a modified truss pattern was calculated from these landmarks with tMorphGen6c (Sheets 2002; Strauss and Bookstein 1982; Figure 7). The measurements were ln-tansformed and used in a principal components analysis (PCA) with varimax rotation (StatView version 5.0.1 Power PC version ©1992-98 SAS Institute, Inc.) and a discriminant analysis (DA) with all variables entered simultaneously, and classification cross-validated by leaving out each successive observation to test functions created by the other samples (SPSS version 15.0 for Windows® ©2006 SPSS Inc.).
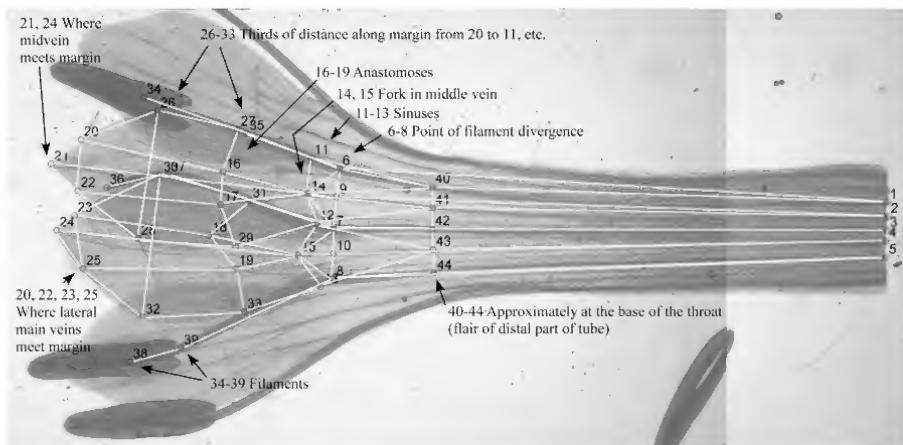
Figure 7. Diagram of interlandmark measurements (white lines) for the corollas. Numbered dots and notes refer to landmarks.

To obtain a more visual idea of how the corolla shapes differ among the populations, the original landmark files were concatenated and used in a relative warp (RW) analysis using the program tpsRelw (1.46, Rohlf 2008; Rohlf 1993), with landmarks for the filaments removed because of artificial variation. Settings were default: Alpha=0, uniform component= complement, scale aligned (centroid size)= 1, projection= orthogonal. This analysis superimposed point configurations for each specimen, then calculated singular values based on the shape differences between configurations (Rohlf 1993).

Since the number and position of lobes on the leaves was too variable to permit the placement of homologous landmarks (Figure 8), a boundary analysis was used instead. One mature leaf, i.e. below the inflorescence but part of the current year's growth, was chosen arbitrarily from each individual and scanned on a Hewlett-Packard ScanJet 3970 or G3010 flatbed scanner at 400 dpi in grayscale, using HP Scanning (version 2.2.1 © 1996-2003 Hewlett-Packard Co.). Individual images were converted to black and white in Adobe® Photoshop® (CS2 Version 9.0 ©1990-2005 Adobe Systems, Inc.). Outlines were captured with TpsDIG (1.40, Rohlf 2004), and 40 elliptic Fourier (EF) harmonics
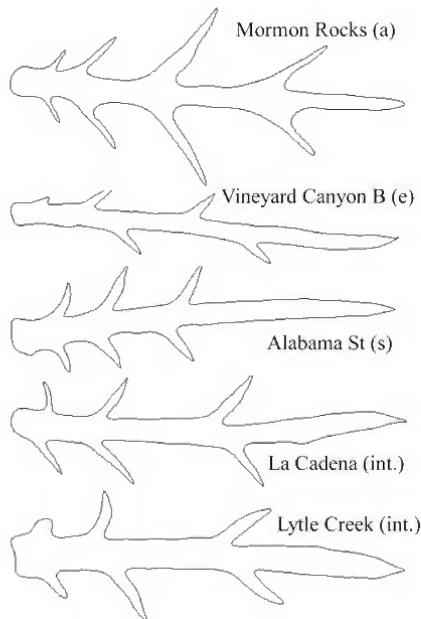
Figure 8. Sample outlines of leaves for each population:

a=subsp. *austromontanum*
e=*elongatum*
s=*sanctorum*
int.=intermediate

were calculated with the program EFA (Rohlf and Ferson 1993; Kuhl and Giardina 1982), although only the first eight harmonics showed variation (see Figure 13) and were used in the analysis. This program was set to be invariant to size (by dividing all points by the square root of the area of the first harmonic) and translation (by subtracting the coordinates of the centroid from each pair of points on the outline), but allowed to vary with rotation and starting position of points. Corrections to make the analysis invariant to rotation and starting position of points both rotate the object so that its major axis is parallel to the x-axis, meaning that final (rotated) position is dependent on the shape of the object. Since this can introduce an artifact into the analysis if there is wide variation among shapes, the corrections for rotation and starting position were not applied (Rohlf and Ferson 1993). In this analysis, all leaves were oriented with the apex up and points were started in approximately the same place. The matrix of EF coefficients was analyzed with PCA (StatView; A1-8, B1-8, C0-8, D1-8) and discriminant analysis, with variables entered simultaneously (SPSS; A1-8, B1-8, C0-8, D1-8).

RESULTS

Principal components analysis of the corolla measurements showed some differentiation among populations (Figure 9). Although 47 components were recovered in the analysis, components 13-47 each explained less than 1% of the variance (not shown). The first axis accounted for 52.6% of the total variation (Table 2), and because nearly all characters had high (>0.5), positive loadings on it, probably referred to corolla size. The Alabama Street population was distinguished from the other populations by PC 1, although there was also
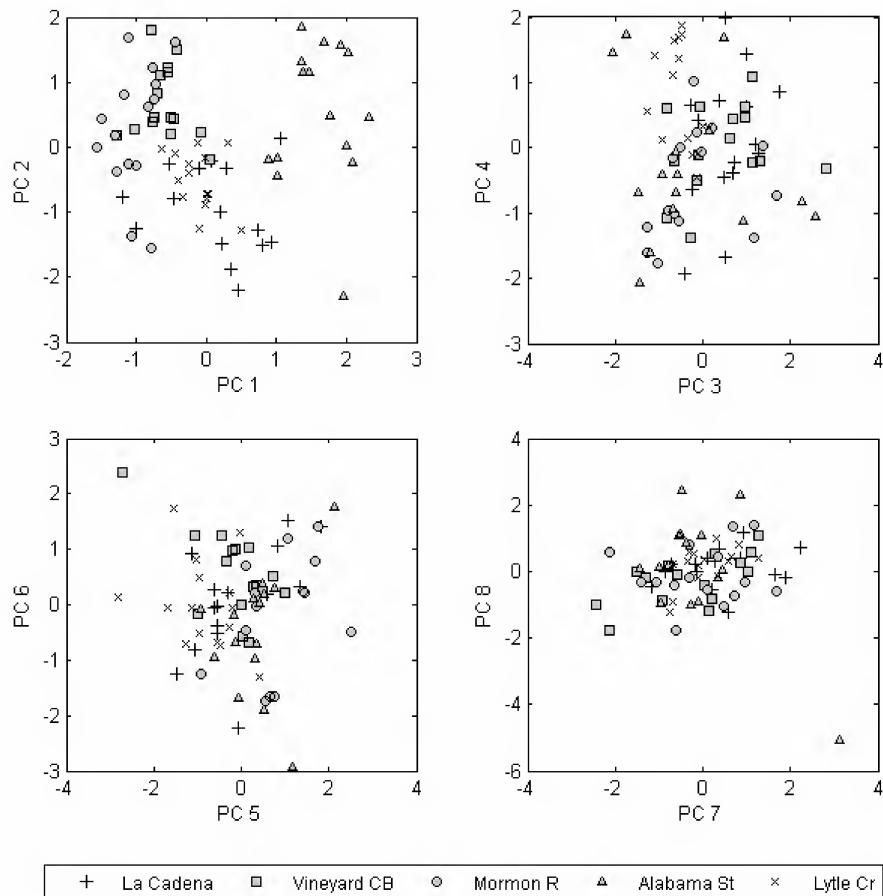
Figure 9. Ordinations of scores of individuals on principal components 1-8, based on corolla measurement data. Note that axes are not necessarily isometric. (La Cadena and Lytle Creek= intermediates. Vineyard CB= subsp. *elongatum*. Mormon R= *austromontanum*. Alabama St= *sanctorum*.)

some separation of the two intermediate populations from a group containing the Vineyard Canyon B and Mormon Rocks populations. PC 2, which was concerned with the distance from the sinus to the filament divergence point, also separated La Cadena and Lytle Creek from Vineyard Canyon B and Mormon Rocks, but with overlap. PC 4 also had high (>0.3) loadings for measurements of the distances from the sinus to the filament divergence point, along with corolla lobe length, and partially distinguished the La Cadena and Lytle Creek populations. Vineyard Canyon B and Mormon Rocks were not readily distinguished by PCA, although PC 6 may show partial differentiation.

Table 2. Eigenvalues, percent variance explained, and some characters described by each axis (based on high loadings) from a PCA of 95 corolla measurements.

PC	Eigenvalue	Variance explained	Characters described
1	49.986	52.6%	Size (loadings ≥0.5 for all but 15 variables); variables associated with tube length have highest loadings (gen. >0.8)
2	8.122	8.5	Distance from sinus to filament divergence point (loadings >0.5)
3	6.735	7.1	Trifurcation position, throat position (loadings generally >0.4)
4	3.867	4.1	Distance from sinus to filament divergence point, anastomoses position (loadings >0.3)
5	3.606	3.8	Shape of the tips of the lobes (loadings >0.4)
6	2.730	2.9	Curvature/asymmetry of corolla lobes and filament lengths 1, 2 (loadings >0.3)
7	2.213	2.3	Possibly corolla asymmetry (loadings >0.3 or <-0.3)
8	1.935	2.0	Width of middle of corolla lobes (loadings >0.4)
9	1.671	1.8	Filament lengths or exsertion, lobe width at base and tip (loadings >0.3 or <-0.3)
10	1.596	1.7	Position of middle sinus and overlap between lobes (loadings >0.3)
11	1.226	1.3	Base of corolla (-.303), tip of right lobe (-0.314)
12	1.006	1.1	Position of trifurcation on left petal, throat (loadings >0.2 or <-0.2)

In contrast to the PCA, the discriminant analysis was able to discriminate all five populations, with an original correct classification rate of 96.0% and a cross-validated rate of 73.3% (random cross-validated data was 20.0% correct; Figure 10, Table 3). All populations had several misclassifications, except for Alabama Street (*sanctorum*), which had 100% correct classification in the cross-validation. Lytle Creek had the worst classification (8 of 15 correct). Function 1 described overall corolla size, and separated the populations fairly neatly into three groups: (1) Alabama Street, (2) La Cadena and Lytle Creek, and (3) Vineyard Canyon B and Mormon Rocks. Function 2 further separated the intermediate populations from Vineyard Canyon B and Mormon Rocks, based on the positions of the sinuses and filament divergence points. Vineyard Canyon B and Mormon Rocks were distinguished by function 3, which referred to the width of the corolla lobes and the position of the midvein trifurcation. La Cadena and Lytle Creek were discriminated by function 3 in combination with function 4, which describes the distance from the throat to the sinuses. Bartlett's Test indicated that all the functions showed significant discrimination between groups (Table 4; Zelditch et al. 2004).

The results of the relative warp analysis largely concurred with the PCA and DA (Figures 11, 12, Table 5). Relative warp 1 distinguished Alabama Street from Vineyard Canyon B and Mormon Rocks, with the La Cadena and Lytle Creek populations in between. Relative warp 2 differentiated the intermediate populations from the others. Vineyard Canyon B and Mormon Rocks were slightly separated on RW 3 and RW 4, while RW 5 partially discriminated La Cadena from Lytle Creek. Relative size of the tube versus the lobes seemed to play a role for RW 1, while characters represented by RW 2 included sinus position and corolla lobe shape (Figure 12).
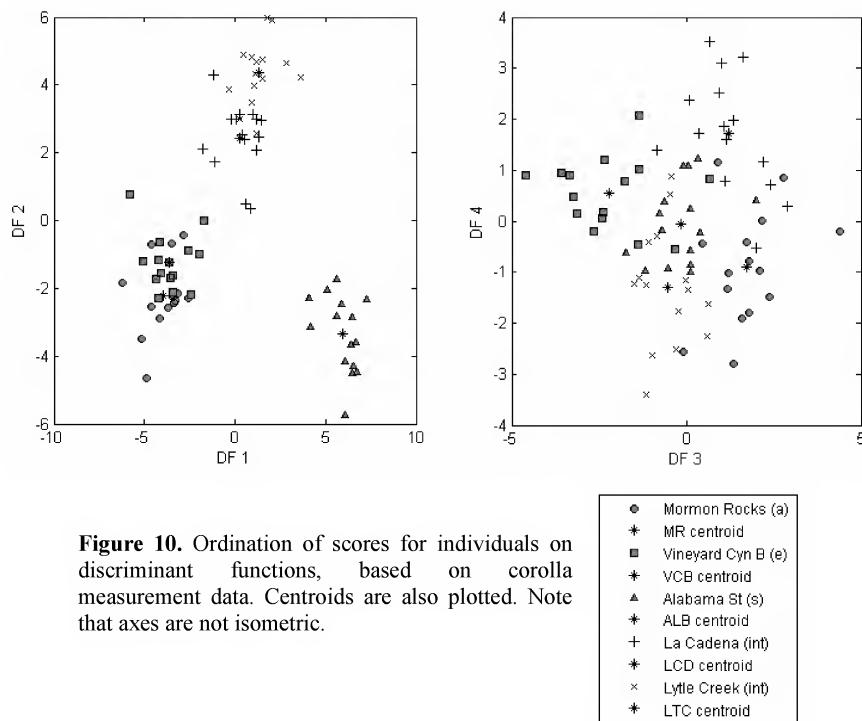
Figure 10. Ordination of scores for individuals on discriminant functions, based on corolla measurement data. Centroids are also plotted. Note that axes are not isometric.

Table 3. Summary of discriminant functions and characters described, from a discriminant analysis using 95 corolla measurements.

Function	Eigenvalue	% of Variance	Canonical Correlation	Characters described (correlations with discriminant functions ≥0.3 unless noted)
1	14.135	53.2	0.966	Corolla size (length and width characters)
2	9.126	34.4	0.949	Sinus and filament divergence positions
3	2.067	7.8	0.821	Corolla lobe width, position of trifurcation (correlations <-0.2)
4	1.236	4.7	0.743	Distance from throat to sinus or furcation

Table 4. Results of Bartlett's Test for discriminant functions.

Function(s)	Wilks' Lambda	Chi-square	DF	p
1 through 4	0.001	389.618	124	0.000
2 through 4	0.014	237.467	90	0.000
3 through 4	0.146	107.821	58	0.000
4	0.447	45.060	28	0.022
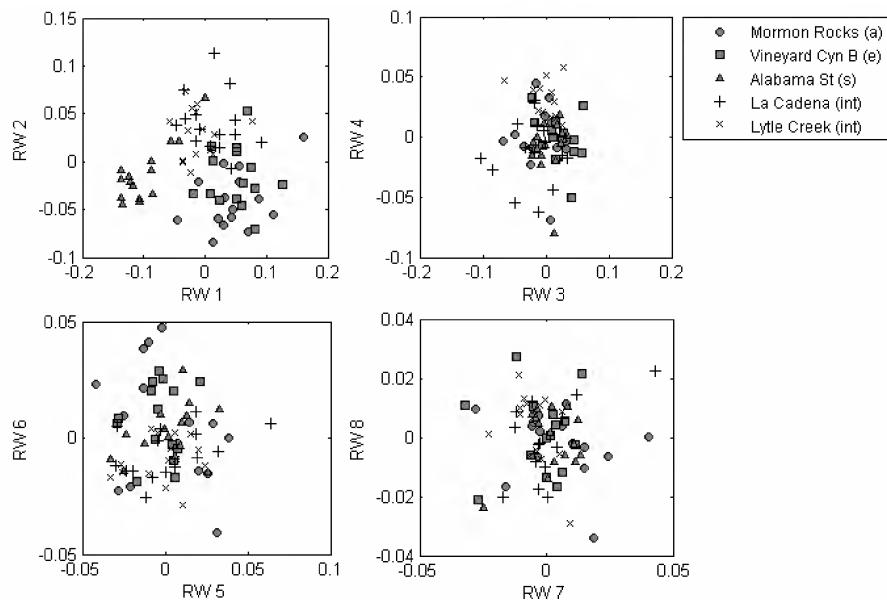
Figure 11. Ordinations of scores of individuals on relative warps 1-8, based on corolla landmark data. Axes are not necessarily isometric.
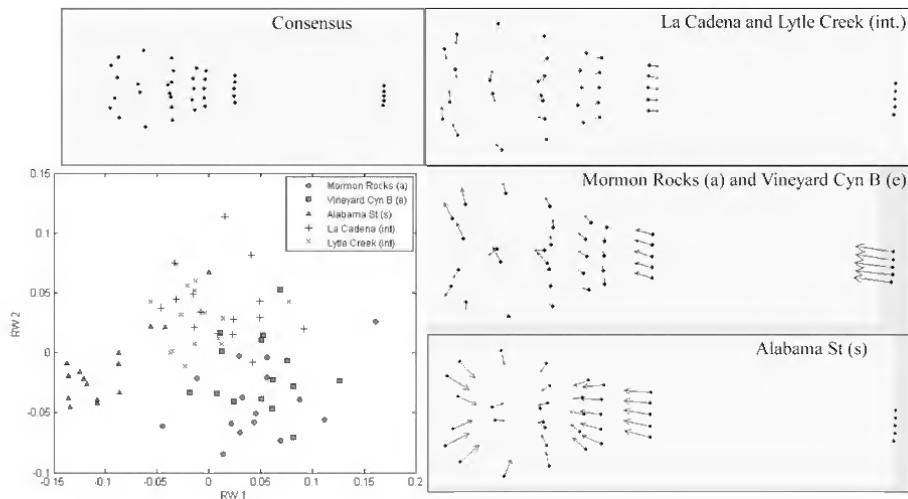
Figure 12. Vector deformations associated with relative warps 1 and 2. The consensus was the average configuration and would correspond to the configuration at the origin of the plot (0,0). The other vector plots show the deformations associated with moving from the consensus shape to the approximate centroid of each of the three main groupings of points in the ordination.

Table 5. Singular values and percent variance explained for the first 20 relative warps, based on 38 corolla landmarks. There were 72 relative warps in total, but warps 21-72 each accounted for less than 0.2% of the variance (not shown).

| warp	Singular value	% Variance	Cum. %	warp	Singular value	% Variance	Cum. %
1	0.57479	46.13	46.13	11	0.07329	0.75	94.52
2	0.36031	18.12	64.25	12	0.06989	0.68	95.20
3	0.26584	9.87	74.12	13	0.06463	0.58	95.78
4	0.22737	7.22	81.33	14	0.06391	0.57	96.35
5	0.1718	4.12	85.45	15	0.05424	0.41	96.76
6	0.14471	2.92	88.38	16	0.05148	0.37	97.13
7	0.11038	1.70	90.08	17	0.05063	0.36	97.49
8	0.10357	1.50	91.58	18	0.04641	0.30	97.79
9	0.09415	1.24	92.81	19	0.04359	0.27	98.06
10	0.08264	0.95	93.77	20	0.03813	0.20	98.26

The first eight elliptic Fourier functions of the leaves appeared to capture most of the variation, and thus only these were used in statistical analyses (Fig. 13). Principal components analysis of the EF coefficients of the leaves showed little differentiation among populations (Figure 14). Component 1 accounted for 21.2% of the variance, PC 2 for 14.9 %, PC 3 for 11.0%, PC 4 for 9.0%, PC 5 for 8.7%, PC 6 for 5.5%, PC 7 for 4.8% and PC 8 for 3.6%. However, the DA distinguished the populations fairly well (Figure 15; Table 6). The original classification rate was 82.7% correct, although the cross-validated rate was 32.0% correct (random cross-validated data was 22.7% correctly classified). While each group had misclassifications in the other four groups, Alabama Street (*sanctorum*) had the highest number of individuals correctly assigned (7 of 15), and Mormon Rocks (*austromontanum*) had the lowest (3 of 15). Function 1 separated Vineyard Canyon B and Mormon Rocks from the other three populations. Function 2 discriminated the intermediates from Alabama Street. Vineyard Canyon B and Mormon Rocks were mostly separated by function 3, and La Cadena and Lytle Creek were distinguished (but with a little overlap) by function 4. Although some discrimination was apparent for all four functions, Wilks' Lambda was significant for only the first function (Table 7; Zelditch et al. 2004).

DISCUSSION

La Cadena and Lytle Creek as hybrid populations

Both corolla and leaf data point to the La Cadena and Lytle Creek populations as morphologically intermediate between subsp. *sanctorum* and the group of subspp. *elongatum* and *austromontanum*, based on the first axis of PCA and DA of both data sets. While morphological intermediacy is not conclusive proof that these populations are of hybrid origin, many hybrids are morphologically intermediate between parents, at least initially (McDade 2000, and citations therein; Jensen et al. 2002). However, it is also very possible that these populations are stable entities, and just as old as the other subspecies, and are simply morphologically intermediate between described subspecies. That the intermediates are of hybrid origin, or that they are not, cannot be shown with these data.
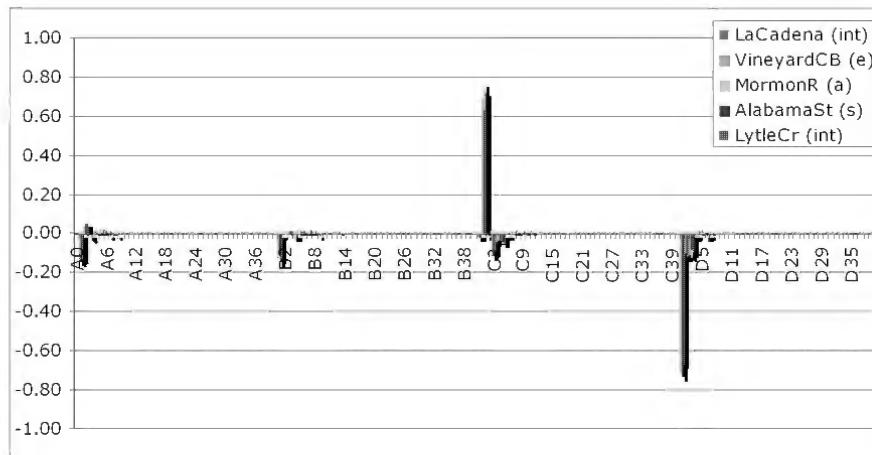
**Figure 13.** Graph showing the amplitudes of each elliptic Fourier coefficient, averaged across each population.
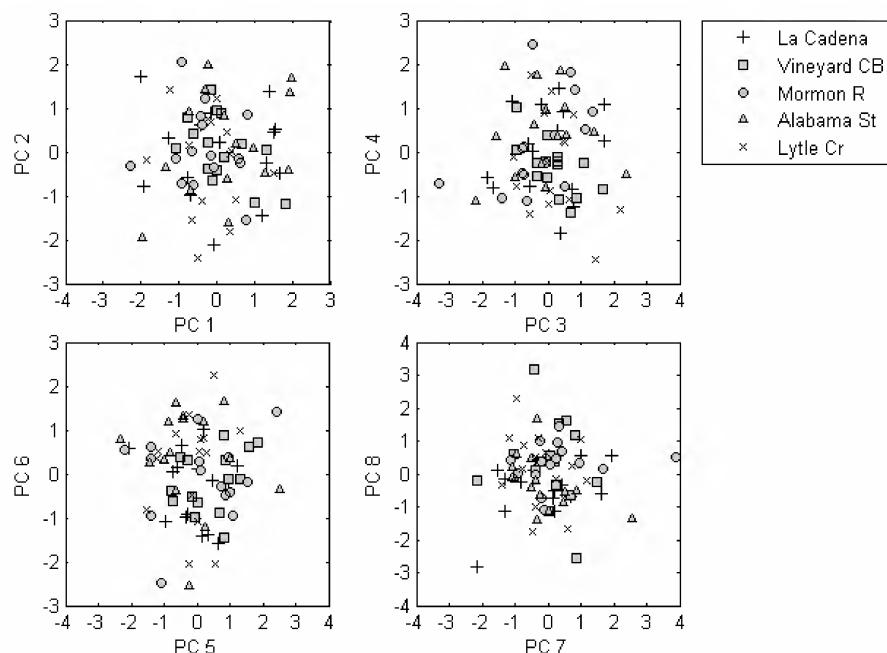

Figure 14. Ordinations of scores of individuals on principal components 1-8, based on elliptic Fourier coefficients for the leaves. Note that axes are not necessarily isometric. (La Cadena and Lytle Creek= intermediates. Vineyard CB= subsp. *elongatum.* Mormon R= *austromontanum.* Alabama St= *sanctorum.*)
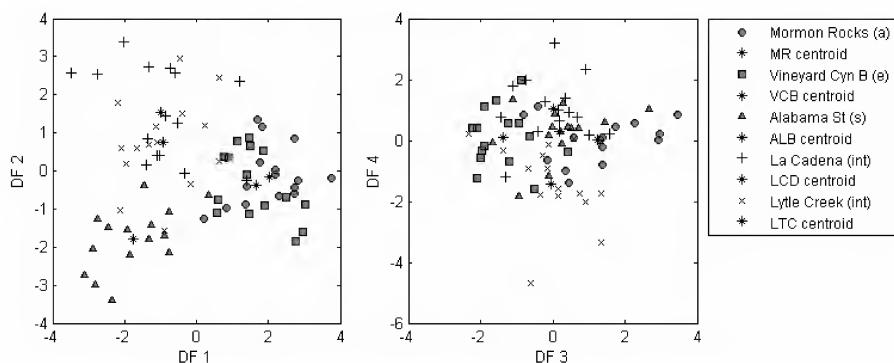
Figure 15. Ordinations of scores of individuals on discriminant functions 1-4, based on elliptic Fourier coefficients for the leaves. Note that axes are not necessarily isometric. Group centroids are also plotted.

Table 6. Summary of discriminant functions for elliptic Fourier coefficients.

Function	Eigenvalue	% of Variance	Canonical Correlation
1	2.521	47.6	0.846
2	1.335	25.2	0.756
3	0.754	14.3	0.656
4	0.681	12.9	0.637

Table 7. Results of Bartlett's Test for discriminant functions.

Function(s)	Wilks' Lambda	Chi-square	DF	p
1 through 4	0.041	175.377	132	0.007
2 through 4	0.145	106.141	96	0.225
3 through 4	0.339	59.496	62	0.567
4	0.595	28.576	30	0.540

It appears that there is little or no reproductive barrier to forming hybrids between subspecies of *E. densifolium*. Brunell and Whitkus (1999a) found that "…populations have not diverged sufficiently to cause a reduction in crossing efficiency with other populations" (250; Brunell and Whitkus 1997). While their results were somewhat inconsistent between years and not all possible crosses were attempted, they did find that many crosses between subspecies produced seed, including crosses between subsp. *sanctorum* and *austromontanum* and crosses between *sanctorum* and *elongatum* (Brunell and Whitkus 1999a).

Neither intermediate population groups well with either subspp. *sanctorum*, *austromontanum*, or *elongatum*, suggesting that plants at the Lytle Creek and La Cadena sites do not fit well into any of these subspecies. However, given that the intermediate populations fall in between subsp. *sanctorum* and the other two subspecies in multivariate

analyses, it seems likely that any hybridization events involved subsp. *sanctorum* for both populations, along with subspp. *elongatum*, *austromontanum*, both, or other subspecies that were not sampled in this study.

How different are the intermediates from the other subspecies?

While plants growing at the Lytle Creek and La Cadena sites can be distinguished, they are morphologically more similar to each other than to subspp. *sanctorum*, *austromontanum*, or *elongatum*. In all analyses, subsp. *sanctorum* and the intermediates as a group were more readily differentiated from each other and from other subspecies than subsp. *elongatum* is from subsp. *austromontanum*. Teasing apart the two hybrid populations, however, was as difficult as discriminating subsp. *elongatum* from subsp. *austromontanum*. Further sampling of additional populations of *E. densifolium* would be necessary to determine more precisely the relationships of the La Cadena and Lytle Creek populations to these and other subspecies (in progress).

Eriastrum densifolium seems to fit well into a model of ecological races, such as those described for North American *Achillea millefolium* (Ramsey et al. 2008). In that study, five non-coding regions of chloroplast DNA and amplified fragment length polymorphisms (AFLPs) showed little structure among populations, leading the authors to conclude that while *A. millifolium* rapidly diversified, it had also expanded its range. Similarly, very little structure was found among populations of *E. densifolium* in Brunell and Whitkus' (1997) study using random amplified polymorphic DNA markers (RAPDs). However, the species is remarkably morphologically diverse, and occurs in a great diversity of habitats, from coastal sand dunes to deserts to montane forests. Morphological adaptations to particular environments may occur at a more rapid rate than molecular evolution or speciation (e.g., Bhagat et al. 2006). Thus, as difficult as ecological races may be to tease apart with molecular techniques, they may be morphologically distinct (Ramsey et al. 2008).

How can these populations be distinguished?

For the populations studied here, corolla size and relative proportions seemed to be the main defining characters (Figures 16, 17). Corollas of the intermediate populations were intermediate in size between subsp. *sanctorum* and the group of subspp. *austromontanum* and *elongatum* (see also La Pré and Pendleton 1988). In the Jepson Manual key (Hickman 1993), the intermediates are likely to lie right in between the corolla lengths described in couplet 4 (<20mm vs. 25-30 mm). For the populations in this study, the total corolla lengths ranged from 11.0 – 18.0 mm in subspp. *austromontanum* and *elongatum*, and from 22.5 – 30.0 mm in subsp. *sanctorum*. The corollas of the intermediates were 13.0 – 21.5 mm long. The La Cadena population had more within-population variation than the Lytle Creek site, based on the sum of ranked (662 vs. 466) or raw (117.1 vs. 37.5) variances calculated for each corolla measurement. The broader range of variation in corolla size is illustrated in Figure 16.

The intermediates also appeared to have a shorter distance between the divergence points of the filaments and the sinuses (Figure 17). Proportionally, these distances were very similar to subsp. *sanctorum*, but the actual distances were smaller because the corollas were smaller (Vineyard Cyn B 0.6 – 1.7 mm; Mormon Rocks 0.3 – 1.7 mm; Alabama St 0.2 – 1.8 mm; Lytle Creek 0.1 – 0.6 mm; La Cadena 0.2 – 0.8 mm). The intermediate
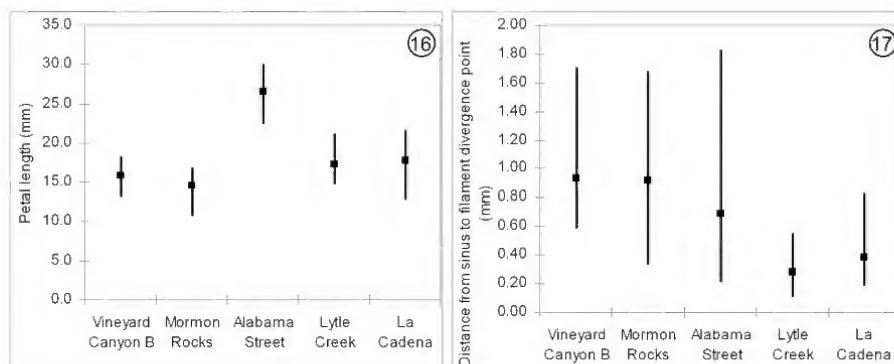
Figure 16-17. Graphs showing mean (squares) and range (bars) of two distinguishing morphological characters. 16. Petal length. 17. Distance from sinus to filament divergence point. Kruskal-Wallis tests on petal lengths and sinus to filament divergence point distances showed significant differences (petal 1: chi-square 47.873, df 4, p<0.001; petal 2: chi-square 47.916, df 4, p<.001; sinus to divergence 1: chi-square 44.736, df 4, p<0.001; sinus to divergence 2: chi-square 47.825, df 4, p<0.001; sinus to divergence 3: chi-square 42.980, df 4, p<0.001). Both Bonferroni and Dunnett T3 post-hoc tests consistently recorded significant differences between Alabama St (*sanctorum*) and the other populations based on petal length (p<0.001), and between the intermediates and Mormon Rocks (*austromontanum*) and Vineyard Canyon B (*elongatum*) based on the distance from the sinus to the filament divergence point (p<0.001).

populations themselves were partially differentiated by the distance from the base of the throat to the sinuses, and by the lengths of the corolla lobes. The positions of midvein trifurcations and the width of the corolla lobes appear to differ somewhat between subspp. *austromontanum* and *elongatum*, but with overlap.

The EF analysis of leaf outlines was harder to interpret biologically (Rohlf and Archie 1984), but the results corroborated the results from the analysis of the corollas. Although PC 1 and DF 1 in the analysis of corollas were associated with size, that was not the case for the leaves, since the leaf outlines were corrected to be invariant to size. Instead, DF 1 may be related to the width of the leaf or rachis, and DF 2 may be related to the amount of lobing near the tip of the leaf. If this is the case, then subsp. *sanctorum* and the intermediate populations would tend to have wider leaves and/or rachi than subspp. *elongatum* or *austromontanum*, and that the intermediates would tend to have more lobes in the distal half of the leaf than does subsp. *sanctorum*. However, leaves are highly variable, and these characters may be difficult to determine in the field.

In conclusion, plants at the La Cadena and Lytle Creek sites did not fit readily into subspp. *sanctorum*, *elongatum*, or *austromontanum*, but instead appeared intermediate between subsp. *sanctorum* and a group containing subspp. *elongatum* and *austromontanum*. The morphological intermediacy suggested that both populations could hybrids (Wheeler 1988; McDade 2000) and, if so, that any or all of these subspecies were likely one of the parents. However, they also could be stable entities as old or older than the other subspecies, that are morphologically intermediate and do not fit into any described subspecies. While each population may be distinguished at least to a degree by one or more morphological characters, molecular evolution has not kept pace with

morphological divergence (Brunell and Whitkus 1997), and additional samples must be added to a larger morphological analysis in order to obtain a more complete picture of the pattern of diversification and adaptation within *E. densifolium.*

LITERATURE CITED

Bhagat, Y., M. G. Fox and M. T. Ferreira. 2006. Morphological differentiation in introduced pumpkinseed *Lepomis gibbosus* (L.) occupying different habitat zones in Portuguese reservoirs. *Journal of Fish Biology* 69 (Suppl. C): 79-94.

Brunell, M. S. and R. Whitkus. 1997. RAPD marker variation in *Eriastrum densifolium* (Polemoniaceae): implications for subspecific delimitation and conservation. *Systematic Botany* 22(3): 543-553.

_____, and _____. 1999a. Analysis of cross-compatibility in *Eriastrum densifolium* (Polemoniaceae). *Plant Systematics and Evolution* 215: 241-254.

_____, and _____. 1999b. Assessment of morphological variation in *Eriastrum densifolium* (Polemoniaceae): Implications for subspecific delimitation and conservation. *Systematic Botany* 23(3): 351-368.

Burk, J. H., C. E. Jones, and J. Wheeler. 1989. New information on the rare Santa Ana River Woolly-Star. *Fremontia* 17(3): 20-21.

Craig, T. 1934. A revision of the subgenus Hugelia of the genus Gilia (Polemoniaceae). *Bulletin of the Torrey Botanical Club* 61: 385-397, 411-428.

Dickinson, T. A., W. H. Parker and R. E. Strauss. 1987. Another approach to leaf shape comparisons. *Taxon* 36(1): 1-20.

Harrison, H. K. 1972. Contributions to the study of the genus *Eriastrum.* II. Notes concerning the type specimens and descriptions of the species. *Brigham Young University Science Bulletin* 16(4): 7.

Hickman, J.C., ed. 1993. The Jepson Manual: higher plants of California. University of California Press, Berkeley and Los Angeles. 1400 p.

Jensen, R. J., K. M. Ciofani and L. C. Miramontes. 2002. Lines, outlines, and landmarks: morphometric analyses of leaves of *Acer rubrum, Acer saccharinum* (Aceraceae) and their hybrid. *Taxon* 51: 475-492.

Jepson, W. L. 1943. Hugelia. Pp. 160-168 in *A Flora of California, Vol. 3 Part II.* University of California, Berkeley, California.

Kramer, K. J. 1987. Endangered and threatened wildlife and plants; endangered status for *Eriastrum densifolium* ssp. *Sanctorum* (Santa Ana River Woolly-Star) and *Centrostegia leptoceras* (Slender-horned Spineflower). *Federal Register* 52(187): 36265-36270.

Kuhl, F. P. and C. R. Giardina. 1982. Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing* 18: 236-258.

La Pré, L. and M. H. Pendleton. 1988. *Biological assessment of the proposed Glen Helen Sheriff's Training Facility Site.* Unpublished report prepared by Tierra Madre Consultants, Inc. and submitted to San Bernardino County Sheriff's Department, San Bernardino, California.

Marsh, K. G. 1988. Regional biogeography of disjunct plant species in the Santa Ana River canyon area. *Crossosoma* 14(2): 1-13.

Mason, H. L. 1945. The genus *Eriastrum* and the influence of Bentham and Gray upon the problem of generic confusion in Polemoniaceae. *Madroño* 8(3): 65-91.

McDade, L. A. 2000. Hybridization and phylogenetics: special insights from morphology. In *Morphological data in phylogenetic analysis: Recent progress and unresolved problems*, ed. J. Weins, 146-164. Smithsonian Institution Press, Washington, D.C.

McLellan, T. and J. A. Endler. 1998. The relative success of some methods for measuring and describing the shape of complex objects. *Systematic Biology* 47(2): 264-281.

Milliken, J. 1904. A review of Californian Polemoniaceae. *University of California Publications in Botany* 2: 1-71.

Olsson, A., H. Nybom and H. C. Prentice. 2000. Relationships between Nordic dogroses (*Rosa* L. sect. *Caninae*, Rosaceae) assessed by RAPDs and Elliptic Fourier analysis of leaflet shape. *Systematic Botany* 25(3): 511-521.

Premoli, A. C. 1996. Leaf architecture of South American *Nothofagus* (Nothofagaceae) using traditional and new methods in morphometrics. *Botanical Journal of the Linnean Society* 121: 25-40.

Ramsey, J., A. Robertson, and B. Husband. 2008. Rapid adaptive divergence in New World *Achillea*, an autopolyploid complex of ecological races. *Evolution* 62(3): 639-653.

Rohlf, F. J. 1993. Relative warp analysis and an example of its application to mosquito wings. In *Contributions to Morphometrics. Museo Nacionale de Ciencias Naturales,* eds. L.F. Marcus, E. Bello, and A. Garcia-Valdecasas, 131-159. Madrid, Spain.

_____. 2004. TpsDIG, version 1.40. Department of Ecology and Evolution, State University of New York, Stony Brook, NY. http://life/bio.sunysb.edu/morph/.

_____. 2008. TpsRelw, version 1.46. Department of Ecology and Evolution, State University of New York, Stony Brook, NY. http://life/bio.sunysb.edu/morph/.

_____, and J. W. Archie. 1984. A comparison of Fourier methods for the description of wing shape in mosquitoes (Diptera: Culicidae). *Systematic Zoology* 33(3): 302-317.

_____, and S. Ferson. 1993. Elliptic Fourier Analysis (software). Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794. 10/24/92. www.sunysb.edu.

Sheets, H. D. 2002. IMP (Integrated Morphometrics Package) Suite. Dept. of Physics, Canisius College, Buffalo, NY 14208. http://www2.canisius.edu/~sheets/morphsoft.html, or http://www2.canisius.edu/~sheets/moremorph.html. CoordGen6h ©2001 H.D. Sheets. TMorphGen6c ©2000 H.D. Sheets Compiled 2005.

Shipunov, A. B. and R. M. Bateman. 2005. Geometric morphometrics as a tool for understanding *Dactylorhiza* (Orchidaceae) diversity in European Russia. *Biological Journal of the Linnean Society* 85: 1-12.

Strauss, R. E. and F. L. Bookstein. 1982. The Truss: body form reconstructions in morphometrics. *Syst. Zool.* 31(2): 113-135.

Wheeler, J. 1988. Recent ecological investigations and present status of the endangered Santa Ana River Woolly-Star, *Eriastrum densifolium* ssp. *sanctorum* (Milliken) Mason. *Crossosoma* 14(3): 1-17.

Zelditch, M. L., D. L. Swiderski, H. D. Sheets, and W. L. Fink. 2004. Geometric morphometrics for biologists: a primer. Elsevier Academic Press, San Diego, California. 443 p.

Zembal, R. and K. J. Kramer. 1984. The known limited distribution and unknown future of Santa Ana River Wooly-Star (*Eriastrum*). *Crossosoma* 10(5): 1-8.

NEW CALIFORNIA RECORDS OF LICHENS AND LICHENICOLOUS FUNGI

Jana Kocourková

National Museum, Department of Mycology, Václavské nám. 68, 115 79 Praha 1, Czech Republic

jana_kocourkova@nm.cz

Kerry Knudsen

The Herbarium, Dept. of Botany & Plant Sciences, University of California, Riverside, California 92521

kk999@msn.com

James C. Lendemer

Cryptogamic Herbarium, Institute of Systematic Botany, The New York Botanical Garden

Bronx, NY, 10458-5126, USA

jlendemer@nybg.org

-and-

Alan M. Fryday

Herbarium, Dept. of Plant Biology, Michigan State University, East Lansing, MI 48824-1312

fryday@msu.edu

ABSTRACT: Six species of lichens and three species of lichenicolous fungi are reported as new for California: *Anisomeridium polypori, Arthonia macounii, Arthrorhaphis aeruginosa, Botryolepraria lesdainii, Clauzadea monticola, Lecania arizonica, Lepraria lecanorica, Marchandiomyces corallinus,* and *Roselliniella cladoniae. Sphaerellothecium reticulatum* is verified as occurring in California.

INTRODUCTION

In 2006, the checklist of lichens, lichenicolous fungi, and allied fungi of California contained 1575 taxa, thirty-six percent of all taxa reported for North America north of Mexico (Tucker & Ryan 2006). This is of course a snapshot in time that is already obsolete with the publication of the final volume of the Sonoran lichen flora which covers southern California north to Santa Barbara County (excluding only the Mojave Desert). Most of the state has been unexplored by lichenologists. Lichens that are new to the state or new to science are still regularly discovered in California. Even in areas that have been surveyed, like Marin County by the California Lichen Society or the Channel Islands by Charis Bratt and the Sonoran lichen project, new taxa can be discovered. In this paper we report six new lichen species and three species of lichenicolous fungi for California. An additional species is verified as occurring in California.

Five of the six lichens reported in this paper were collected in Limekiln State Park near Big Sur in Monterey County in a coast redwood (*Sequoia sempervirens*) forest. Two of those species were calciphiles, occurring on limestone: *Botryolepraria lesdainii* and

Clauzadea monticola. The sixth lichen species we report, *Lecania arizonica*, was collected in the Mojave Desert.

Lichenicolous fungi are under-collected in California. The three lichenicolous fungi reported were collected on Santa Rosa Island, with one, *Arthrorhaphis aeruginosa,* also collected in Marin County on the recent International Association for Lichenology (IAL) excursion.

Seven of the species reported new to California are part of the temperate lichen biota of the northern hemisphere. This flora is especially well-represented in the mountains of Arizona and in California, though individual species may be more abundant in the Pacific Northwest or eastern North America, or Europe. For instance, we have recently collected second records for California of *Bilimbia sabuletorum* (Schreb.) Arnold (*Knudsen 9955.1 & Kocourková,* UCR, PRM) and *Hertelidea botryosa* (Fr.) Printzen & Kantvilas on redwood bark in Limekiln State Park (*Knudsen 9974 & Kocourková*, NY, UCR) and *Calicium corynellum* (Ach.) Ach. on granite in the San Jacinto Mountains (*Knudsen 10000 & Kocourková*, UCR; *Kocourková & Knudsen,* PRM). These three species are more common elsewhere in their temperate distribution, but rare in California.

The remaining two species we report, *Lecania arizonica* and *Lepraria lecanorica,* are currently considered endemic to Arizona and California. They were recently described and may be more widespread.

The publication of new state and North American records as well as the results of floristic surveys in such journals as *The Bulletin of the California Lichen Society* and *Evansia,*, and the deposition of the collections in public herbaria, are important contributions to the eventual publication of a new North America lichen flora.

The Species

Anisomeridium polypori (Ellis & Everh.) M. E. Barr is a cosmopolitan crustose lichen with a *Trentepohlia* photobiont reported from Africa, Asia, Australia, Europe and North America (Aptroot 1999). It occurs on numerous substrates, including a variety of trees and wood, dead liverworts and polypores, and even brick. It prefers shade and high humidity. Fittingly, it is reported new to California from a grove of coastal redwoods in deep shade along a perennial stream on the old bark of the Pacific maple (*Acer macrophyllum*). Usually *A. polypori* is sterile and is easily recognized by its conical pycnidia with long necks which exude packets of conidia in persistent gelatinous gobs. Both microconidia and ascospores were found in the California specimen.

Cited Specimen: Monterey County: Limekiln State Park, Hare Creek, 36° 00' 38" N, 121° 31' 00" W, 30 m, July 21 2008, *Kocourková & Knudsen* (PRM) & *Knudsen 9955.2 & Kocourková with Mike Walgren & Lisa Andreano* (UCR).

Arthonia macounii G. Merr., Ottawa Naturalist 28: 36 (1914). Holotype: Macoun, Sidney, on young firs (FH!)
    Arthothelium macounii (G. Merr.) W. Noble, Mycotaxon 28 (1): 91 (1987).

Arthonia macounii is a crustose lichen with a *Trentepohlia* photobiont. It was collected on the small branches of the California Bay tree (*Umbellaria californica*) in the understory of a coast redwood forest with *Arthonia cinnabarina* (DC.) Wallr. The species

is distinguished by hyaline ascospores 20–38 × 10–14 μm, clavate in maturity and darkening, with an enlarged, undivided end cell and 4-6 transverse septa divided by 1-2 longitudinal septa. The hypothecium is pale and the epihymenium is brownish-violet with granules becoming orange-red to magenta when the slide is flooded with potassium hydroxide (K). *Arthothelium reagens* Coppins & P. James, collected in Scotland, appears to be a synonym but the holotype was not examined. It is now recognized that both transverse-septate ascospores and muriform ascospores both occur in *Arthonia* s. str. Species described in *Arthothelium* are being transferred to *Arthonia* as they are studied (Grube 2007) and we thus recognize this taxon as *Arthonia macounii* rather than *Arthothelium macounii*.

Cited Specimen: Monterey County: Limekiln State Park, Hare Creek, 36° 00' 38" N 121° 31' 00" W, 30 m, July 21 2008, *Knudsen 9960 & Kocourková with Mike Walgren & Lisa Andreano (*UCR).

Arthrorhaphis aeruginosa R.Sant. & Tønsberg is a lichenicolous fungus parasitic on *Cladonia* species, especially *Cladonia coniocraea*, usually infecting the squamules (Santesson & Tønsberg 1994). It turns the host *Cladonia* a blue color that is quite distinctive, ultimately depleting the algal layer of the host. It can be determined from the color of the infection. It produces apothecia with acicular hyaline ascospores 80–120 × 2.5–5μm with 12-28 septa or pycnidia but they are found only occasionally. It was originally described from Norway, western Scotland, and coastal Washington and Oregon. The new reports from California extend its range south along the coast of western North America. The Marin County specimen was fertile.

Cited Specimens: Marin County: Golden Gate National Park, West Ridgecrest Blvd., west of Rock Springs, on *Cladonia* species, July11 2008, *Kocourková & Knudsen, IAL Excursion* (PRM); Santa Barbara County: Santa Rosa Island, Channel Islands National Park, north slope of Black Mountain, first canyon west of truck trail, 267 m, 33° 58' 58" N 120° 4' 4" W, on *Cladonia pyxidata*, July 18 2007, *Kocourková and Knudsen* (PRM, UCR).

Botryolepraria lesdainii (Hue) Canals, Her.-Mar., Gómez-Bolea & Llimona is a pale lime-green or olive-green leprariod lichen forming thick cottony sterile patches on limestone and concrete in shade with high relative humidity. It is spot-test negative, containing only terpenoids. It has been reported from Africa (Canary Islands), Asia, Europe and North America (Tønsberg 2007b). It was collected in California in a redwood forest on limestone. It is recently reported as being common in eastern North America on suitable calcareous habitat (*Lendemer* in press). It is a beautiful lichen and easily recognized in the field.

Cited Specimen: Monterey County: Limekiln State Park, 36° 00' 54" N 121° 31' 15" W, 36 m, July 21 2008, on limestone and decayed concrete, *Knudsen 9973 & Kocourková with Mike Walgren & Lisa Andreano*(NY, PRM, UCR).

Clauzadea monticola (Ach. ex Schaer.) Hafellner & Bellem. has smal lecideine apothecia with a thin whitish thallus discoloring the substrate, a *Porpidia* ascus stain, simple hyaline ascospores 6.5–12 × 3.5–7 μm, dark hypothecium, and is spot test negative. It looks like a *Sarcogyne*. It is a calciphile and is common in limestone quarries in the Czech Republic, for instance, and occurs from Europe, through Greenland and

eastern North America to Alaska (Thomson 1997). It was abundant on hard limestone at Limekiln State Park in a redwood forest.

Cited Specimen: Monterey County: Limekiln State Park, 36° 00' 54" N, 121° 31' 15" W, 36 m, July 21 2008, on limestone and decayed concrete, *Knudsen & Kocourková 9970 with Mike Walgren & Lisa Andreano* (UCR).

Lecania arizonica B.D. Ryan & van den Boom was described from the Sonoran desert in Arizona (van den Boom & Ryan 2004). It is a crustose lichen with numerous small dark red apothecia with a whitish margin and occurs on sandstone and granite. The one-septate hyaline ascospores are 10–20 × 4–6 um. It is reported new to California from the UC Sweeney Granite Mountains Desert Research Center in the Mojave Desert, where it is rare.

Cited Specimen: San Bernardino County: Granite Mountains, near lower Sibyl Allanson trail, 34° 47' 01" N, 115° 39' 43" W, 1333 m, on decaying granite outcrop above wash, June 7 2008, *Knudsen 9704* (UCR).

Lepraria lecanorica Tønsberg is a leprose lichen described and reported from montane Arizona (Tønsberg 2004b). It was collected on basic rock in a shady, humid redwood forest above a perennial creek. It contains lecanoric acid and is KC+ reddish pink.

Cited Specimen: Monterey County: Limekiln State Park, Hare Creek, 36° 00' 38" N, 121° 31' 00" W, 30 m, July 21 2008, *Knudsen 9941 & Kocourková with Mike Walgren & Lisa Andreano* (UCR, NY).

Marchandiomyces corallinus (Roberge) Diederich & D. Hawksw. is a lichenicolous fungus and an anamorphic basidiomycete occurring on a wide variety of lichens, with abundant bright reddish or pink red sclerotia emerging from the host. It is common and widespread in Europe with scattered reports from North America (Diederich 2003). We have been looking for it in southern and central California for several years, where it appears to be rare.

Specimen cited: Santa Barbara County: Santa Rosa Island, Channel Islands National Park, along Burma Road, 33° 56' 40" N, 120° 7' 4" W, 462 m, on *Teloschistes chrysophthalmus* on branches of *Bacchris pilularis*, among old *Quercus tomentella*, July 20 2007, *Kocourková & Knudsen* (PRM 909661, UCR).

Roselliniella cladoniae (Anzi) Matzer & Hafellner is a lichenicolous fungus on the squamules of *Cladonia* with black ascomata, 4-spored asci, mostly simple large ascospores (with occasional 1-septate ascospores) 35–50 × 12–15 um, becoming brown at maturity. It is known from Europe and South America. This is the fifth report from North America (Diederich 2003). It is probably frequent in California.

Specimen cited: Santa Barbara County, Santa Rosa Island, Channel Islands National Park, south side above the pacific on eastern part of Sierra Pablo Ridge,33° 56' 47" N, 120° 0' 37" W, 219 m, on undescribed *Cladonia* of *C. cervicornis* group on soil, July 19 2007, *Kocourková & Knudsen* (PRM 909680, UCR).

Sphaerellothecium reticulatum (Zopf) Etayo, originally named *Echinothecium reticulatum* Zopf, is a lichenicolous fungus that is found on *Parmelia* s. str. It forms a

thin hyphal net and can be confused with *Lichenostigma* species but differs especially by the pseudothecia with setae (hair-like appendages) and the lack of spherical cells in the hamathecium. A previous report from California was doubtful because the host was a *Hypogymnia* (Tucker & Ryan 2006). This collection verifies its occurrence in California.

Cited Specimen: Riverside County: San Jacinto Mountains, San Bernardino National Forest, north fork of San Jacinto River, 33° 47' 56" N, 116° 44' 06" W, 1700 m, on *Parmelia saxatalis* on shaded granite outcrop, July 28, 2008, *Kocourková & Knudsen* (PRM, UCR).

Acknowledgments

Aptroot, A. 1999.Notes on taxonomy, distribution and ecology of *Anisomeridium polypori. Lichenologist* 31(6): 641–642.

Diederich, P. 2003. New species and new records of American lichenicolous fungi [Neue Arten und neue Funde von amerkanischen lichenicolen Pilzen]. *Herzogia* 16: 41-90.

Grube, M. 2007 (2008). *Arthonia.* In *Lichen flora of the greater Sonoran Desert region, Vol. 3,* eds. T.H. Nash, III, C. Gries, and F. Bungartz, 39-61. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Lendemer, J. C. in press. New and interesting records of lichens and lichenicolous fungi from New Jersey and Pennsylvania. *Evansia.*

Santesson, R. & T. Tønsberg. 1994: *Arthrorhaphis aeruginosa* and *A. olivaceae*, two new lichenicolous fungi. *Lichenologist* 26(3): 295–299.

Thomson, J.W. 1997. *American arctic lichens. 2. The Microlichens.* The University of Wisconsin Press, Madison. 675 pp.

Tønsberg, T. 2004. *Lepraria.* In *Lichen flora of the greater Sonoran Desert region, Vol. 2,* eds. T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries and F. Bungartz, 322-329. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Tønsberg, T. 2007 (2008). *Botryolepraria.* In *Lichen flora of the greater Sonoran Desert region, Vol. 3,* eds. T.H. Nash, III, C. Gries, and F. Bungartz, 112-113. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Tucker, S. and B. Ryan. 2006. Revised catalog of lichens, lichenicoles, and allied fungi in California. *Constancea* 84: 1-275 + 1-52.

van den Boom, P.P.G and B.D. Ryan. 2004. *Lecania* In *Lichen flora of the greater Sonoran Desert region, Vol. 2*, eds. T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries and F. Bungartz, 143-171. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Note: Due to an error on the editor's part, an unrevised version of the following article was inadvertently printed in Crossosoma 33(2). The correct version follows. The editor deeply regrets the error.

PLANT SUCCESSION IN THE EASTERN MOJAVE DESERT: AN EXAMPLE FROM LAKE MEAD NATIONAL RECREATION AREA, SOUTHERN NEVADA (revised)

Scott R. Abella
Public Lands Institute and School of Life Sciences
University of Nevada Las Vegas
4505 S. Maryland Parkway
Las Vegas, NV 89154-2040
scott.abella@unlv.edu

Alice C. Newton
National Park Service
Lake Mead National Recreation Area
601 Nevada Way
Boulder City, NV 89005

-and-

Dianne N. Bangle
Public Lands Institute
University of Nevada Las Vegas
4505 S. Maryland Parkway
Las Vegas, NV 89154-2040

ABSTRACT: Plant succession remains a poorly understood process in the Mojave Desert, yet knowledge is needed in this area where increasing human populations may amplify disturbance frequencies and intensities. In a retrospective study, we examined plant communities on two pipeline corridors, one cleared in 1998 and one in 1968 to supply water to metropolitan Las Vegas, Nevada. We also evaluated the effectiveness of restoration treatments (raking soil surfaces, spreading artificial desert varnish, and planting four species of native shrubs) applied by the National Park Service on the 1998 corridor to enhance recovery of *Larrea tridentata* communities. Plant cover was sparse (< 5%) on the untreated 1998 corridor eight years after clearing, with a mean shrub density of only 99/ha. On the restoration-treated area, however, *L. tridentata* established at a density of 300/ha, 36% of the density of an adjacent control area. Restoration treatments also made the corridor less visually distinct from surrounding *L. tridentata* communities. Even 38 years after clearing, the older corridor was dominated by species such as *Stephanomeria pauciflora* and *Encelia farinosa*, which are classified as early colonizers in the Mojave Desert. Our findings concur with long recovery estimates after vegetation-removing disturbances given in the literature, but suggest that ecological restoration has potential for manipulating the speed and trajectory of plant succession in the Mojave Desert.

KEYWORDS: disturbance, ecological restoration, *Encelia farinosa*, *Hymenoclea salsola*, *Larrea tridentata*, *Stephanomeria pauciflora*, vegetation.

INTRODUCTION

Mining, military activities, off-road vehicles, agriculture, livestock grazing, and land clearing for linear corridors (e.g., roads, power lines) are some of the many types of human disturbances impacting Mojave Desert ecosystems (Lovich and Bainbridge 1999). Plant succession (rate and species composition) following these disturbances can vary with disturbance type (Webb et al. 1987), disturbance size (Hunter et al. 1987), precipitation (Brum et al. 1983), time since disturbance (Carpenter et al. 1986), and also with other less-documented factors such as soil type (Lathrop and Archbold 1980). *Larrea tridentata* (DC.) Cov. communities, which are a dominant vegetation type in the Mojave Desert, have generally taken decades to more than centuries to approximate pre-disturbance plant composition (Lovich and Bainbridge 1999).

Vasek (1979/1980) documented plant succession in the southeastern Mojave Desert nine years after land clearing for a highway borrow pit in southern California. He found that early colonizers included *Ambrosia dumosa* (A. Gray) Payne, *Encelia frutescens* (A. Gray) A. Gray, *Stephanomeria pauciflora* (Torrey) Nelson, and *Porophyllum gracile* Benth. These species exhibited 19-177 times greater densities in the disturbed pit bottom than in adjacent *Larrea tridentata* communities. Vasek (1983) further classified Mojave Desert perennial species into three main successional categories: early colonizers that respond strongly and positively to disturbance and have short individual life spans (e.g., *Hymenoclea salsola* A. Gray, *S. pauciflora*, *Encelia* spp.), long-lived opportunistic species important in older communities but also exhibiting pioneering ability (e.g., *A. dumosa*, *Opuntia bigelovii* Engelm.), and long-lived perennials that recover slowly from disturbance (e.g., *L. tridentata*). Vasek (1983) also noted that many early colonizers after human disturbance are abundant in frequently disturbed "natural" habitats such as washes, and that annual plants occur in both early and late-successional communities.

Specific questions about succession, such as factors affecting its rate and trajectory, remain poorly understood in the Mojave Desert, and in deserts in general (Bolling and Walker 2000). This hinders ecological management in deserts, where increasing human populations may intensify disturbance levels (Kemp and Brooks 1998; Lovich and Bainbridge 1999). In a retrospective study in the eastern Mojave Desert, we assessed plant community and soil characteristics on two water pipeline corridors cleared of surface soil and vegetation eight (1998) and thirty-eight (1968) years before this study. The National Park Service also applied restoration treatments designed to speed recovery of *Larrea tridentata* communities on part of the 1998 corridor. Both corridors cross National Park Service land (Lake Mead National Recreation Area [LMNRA]) and were constructed to supply water to the metropolitan Las Vegas Valley. Since further water developments are planned to occur within LMNRA, this study was intended to evaluate potential for natural succession and ecological restoration of these disturbances. Additionally, our study adds site-specific successional data needed to build general theories of succession for the Mojave Desert. We sought to answer the following questions at this site: (1) What is species composition, shrub density, and species richness on corridors cleared in 1998 and 1968 relative to adjacent *L. tridentata* communities? (2) On the 1998 corridor, do soil properties differ among treatments and below *L. tridentata* compared to interspaces between shrubs? (3) How does species composition on this site after disturbance compare with other successional sequences described for the Mojave Desert?

METHODS

Study Area and Pipeline Treatments

This study was conducted in LMNRA, Clark County, Nevada, 30 km east of the city of Las Vegas at an elevation of 400 m (UTM 696000 m E, 3993000 m N; zone 11; NAD83). The study area consisted of a 0.21-ha area in each of four adjacent locations: a 1998 corridor receiving no restoration treatments (hereafter untreated 1998 corridor), an adjacent section of the same corridor that received restoration treatments (hereafter treated 1998 corridor), an adjacent *Larrea tridentata* community off the corridor that served as a control, and a corridor cleared in 1968 adjacent to the 1998 corridor (Figure 1). This study of a pre-existing disturbance and an operational management activity is limited by a lack of replication; however, the study area comprises one landform (an alluvial fan) and one soil association (Carrizo-Carrizo-Riverbend, primarily consisting of Typic Torriorthents; Lato 2006). This supports an assumption that potential differences among the four areas primarily result from their successional age or the restoration treatments, rather than from pre-existing environmental differences. Both the treated and the untreated 1998 corridor were cleared by blading with heavy equipment, with the upper 20 cm of soil stockpiled and reapplied after construction. The 20-cm depth may have varied slightly depending on rockiness or other factors. The 1968 corridor also was cleared by mechanical blading, but topsoil was not replaced (David Connally, Southern Nevada Water Authority, personal communication).

Restoration treatments applied by the National Park Service in January-February 1999 to the 1998 corridor included hand-raking the soil surface after soil replacement to re-spread rocks, applying artificial desert varnish (product name = permeon, Soil-Tech, Inc., Las Vegas, NV) evenly to the soil surface for color restoration, and planting *Larrea tridentata* (96 plants), *Ambrosia dumosa* (12 plants), *Opuntia basilaris* Engelm. & J. Bigelow (9 plants), and *Acacia greggii* A. Gray (2 plants). Desert varnish is a brown-black coat given its color by iron and manganese oxides. This varnish commonly forms on stable surfaces on volcanic rock, a process that is hastened by the chemical application of artificial desert varnish (Moore and Elvidge 1982). The planting treatment is detailed in Newton (2001). By 2001, no planted *A. greggii* or *A. dumosa* were alive, but survival was 92% for *L. tridentata* and 100% for *O. basilaris* (Newton 2001).

Annual precipitation from 1999-2005 after clearing of the 1998 corridor averaged 105% of the long-term (32 yr) mean (14 cm/yr), measured at Willow Beach, AZ, 26 km south of the study site (Western Regional Climate Center, Reno, NV). As is typical of the Mojave Desert, however, precipitation ranged widely from 27% (2002) to 205% (2004) of the long-term mean among years.

Field Sampling

Between 31 August and 25 October 2006, we delineated a 30 × 70 m section in the centers of each of the four areas. Within these sections, we randomly established a 10 × 70 m transect divided into seven 10 × 10 m (0.01 ha) plots. Using simple random sampling, we selected three plots in each section for sampling. Within each plot, we established six 1 × 1 m subplots per plot located at the plot corners and at the midpoints (5 m) of southern and northern plot lines. We visually estimated areal percent cover of each plant species rooted in subplots using a 1-m^2 frame divided into 25, 0.04 m^2
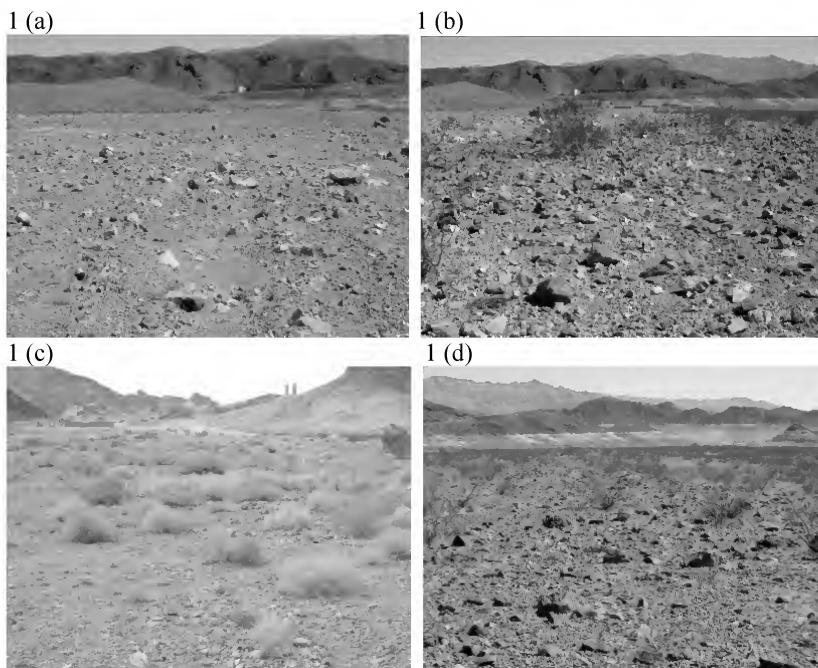
Figure 1. Views of (a) bladed 1998 water pipeline corridor that received no restoration except for soil replacement; (b) the same corridor that received the restoration treatments of raking the soil surface, applying artificial desert varnish, and planting four species of native shrubs in addition to soil replacement; (c) 1968 water pipeline corridor; and (d) control area (note the intact desert pavement) adjacent to the corridors, Lake Mead National Recreation Area, southern Nevada. Photos by S.R. Abella, 8 October 2007.

compartments. We also surveyed whole plots on a presence/absence basis for species not occurring in subplots. Our sampling time in late summer and fall was not designed to capture live annuals, but we recorded standing dead annuals in subplot and plot sampling. Live shrubs, including seedlings, were counted on each plot. Nomenclature and native/exotic species classifications follow Baldwin et al. (2002). To compare soils among the control and the treated and untreated 1998 corridor, we collected a 0-10 cm soil sample in an interspace ($\geq$ 1 m away from any shrub) at the northwestern and southeastern corners of each plot and composited these samples on a plot basis. We also selected a dominant *Larrea tridentata* on each plot on the control and on the treated 1998 corridor (the untreated corridor contained no *L. tridentata*) and collected four, 0-10 cm soil samples (composited on a plot basis) halfway between the main stem and the canopy edge.

Laboratory and Data Analysis

Air dried < 2 mm fractions of soil samples were analyzed for pH (saturated paste), total P and K (Olsen NaHCO$_3$ method), total C and N (Leco C/N analyzer), and texture (hydrometer method). We compared mean (*n* = 3 for each area) species richness and total mean shrub density among the control, treated and untreated 1998 corridor, and the 1968

corridor using one-way analysis of variance and Tukey's test in JMP (SAS Institute 2004). Analysis of variance also was used to compare interspace soils among the control and 1998 corridor areas. For the control and the treated 1998 corridor, we used paired *t* tests to compare soil properties between interspaces and below *Larrea tridentata*. Statistical results should not be extrapolated to other sites since treatments were not replicated, but mean comparisons are presented as interpretational aids.

RESULTS

1998 Corridor

Exotic species richness/m^2 was similar between treated and untreated areas in the 1998 corridor but was greater than in the control (Figure 2). Total species richness/100m^2 was similar among treatments, ranging from 8-9.3 species. The exotic annual grasses *Schismus* spp. exhibited the highest relative cover on the 1998 corridor compared to the control, but total absolute cover for all species on the corridor was only 5-6% (Figure 3). Relative cover of the native annual *Plantago ovata* Forsskal was highest in the control, intermediate in the treated corridor, and lowest in the untreated corridor. Perennial forbs and grasses were sparse or absent from all treatments. Shrub density was eight times higher in the control than in the untreated corridor, which contained no *Larrea tridentata* (Figure 4). *Ambrosia dumosa* and *Encelia farinosa* Torrey & A. Gray were the only shrubs inhabiting the untreated corridor, and these species did not occupy plots on the treated corridor or on the control. *Larrea tridentata* exhibited a density of 300/ha on the treated corridor, which was 36% of the density on the control.

In interspaces, soil properties were similar among the treated, untreated, and control areas except for K, which was significantly greater on the untreated corridor than on the control (Table 1). Sand concentration was 10% higher and silt 9% lower on the untreated corridor compared to the control, but all soils were still sandy loams. P and K both tended to be greater below *Larrea tridentata* than in interspaces for the treated corridor and the control, but the only difference that was statistically significant ($p < 0.05$) was for P for the control.

1968 Corridor

Exotic species richness was lowest in the 1968 corridor relative to the control or the 1998 corridor, and total richness/100 m^2 was comparable to both the 1998 corridor and the control (Figure 2). Similar to the 1998 corridor, *Plantago ovata* was a major contributor to relative cover, although *Stephanomeria pauciflora* exhibited the highest relative cover. Total shrub density averaged 3134/ha, 31 times more than the untreated 1998 corridor, nine times more than the treated 1998 corridor, and four times more than the control. *Stephanomeria pauciflora* and *Hymenoclea salsola* contributed 76% of the total shrub density.
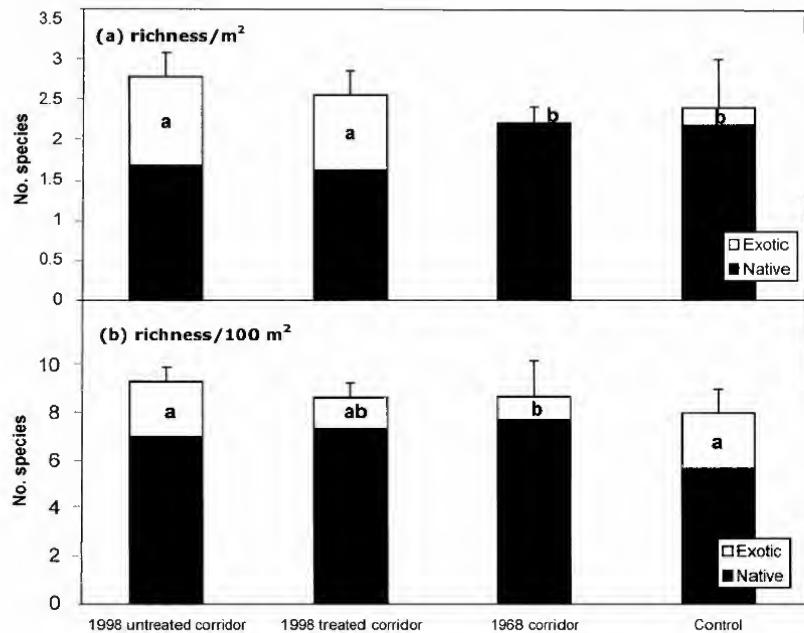
Figure 2. Mean plant species richness at (a) 1 m^2 and (b) 100 m^2 scales among water pipeline corridors and a control area, Lake Mead National Recreation Area, southern Nevada. Error bars are 1 SD for total mean richness. In comparisons within native or exotic categories, only exotic species per m^2 and per 100 m^2 differed significantly ($p < 0.05$) among the four areas.
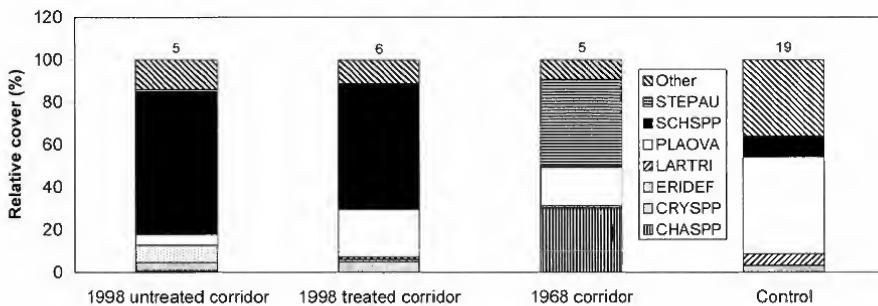
Figure 3. Relative cover of dominant plant species and genera among water pipeline corridors and a control area, Lake Mead National Recreation Area, southern Nevada. CHASPP = *Chamaesyce* spp., CRYSPP = *Cryptantha* spp., ERIDEF = *Eriogonum deflexum*, LARTRI = *Larrea tridentata*, PLAOVA = *Plantago ovata*, SCHSPP = *Schismus* spp., and STEPAU = *Stephanomeria pauciflora*. Numbers at the top of each bar represent total mean absolute % cover.

Table 1. Comparison of 0-10 cm soil properties among treatments and between interspaces and below *Larrea tridentata* within treatments on an eight-year-old (1998) water pipeline corridor, Lake Mead National Recreation Area, southern Nevada.

Property	Untreated corridor		Treated corridor[1]		Control	
	Interspace	*Larrea*	Interspace	*Larrea*	Interspace	*Larrea*
pH	8.1±0.1[2]	—[3]	8.1±0.2	8.1±0.1	8.1±0.1	7.9±0.1
P (mg/kg)	4.0±1.2	—	3.5±0.7	3.7±0.8	4.1±1.6	11.5±2.9
K (mg/kg)	555±13a	—	491±62ab	575±204	**400±61b**	**552±42**
C (mg/kg)	942±35	—	716±118	954±107	686±180	736±90
N (mg/kg)	27±5	—	37±14	43±8	57±27	50±15
Sand (% wt.)	70±2a	—	65±3b	67±4	60±1b	66±6
Silt (% wt.)	24±1b	—	29±3a	27±3	33±2a	28±5
Clay (% wt.)	6±2	—	6±0	6±1	7±1	6±2

[1] Restoration treatments included raking the soil surface, applying artificial desert varnish, and planting four species of native shrubs.
[2] Vales are mean ± SD ($n = 3$ within each treatment and canopy combination). Letters within a row compare means among treatments for interspaces only. Values in bold denote significant differences at $p < 0.05$ between interspaces and below *Larrea tridentata* within treatments.
[3] Not measured because *L. tridentata* did not occur in this treatment.
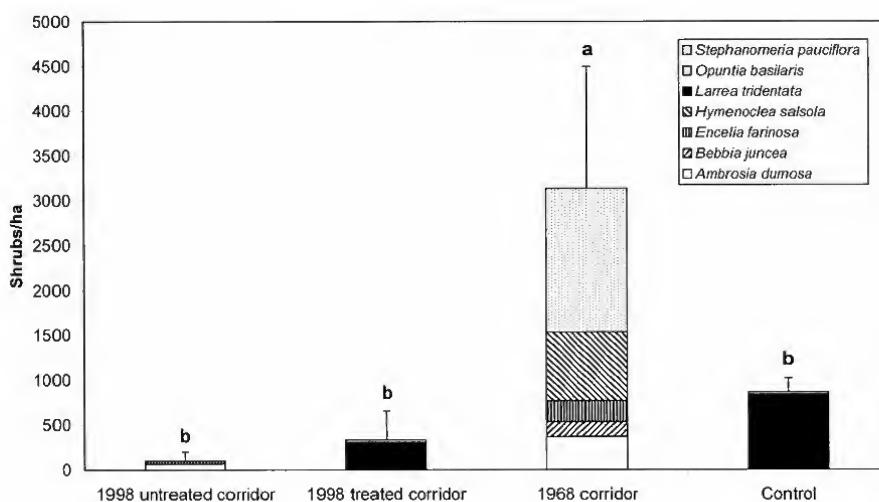

Figure 4. Shrub densities among water pipeline corridors and a control area, Lake Mead National Recreation Area, southern Nevada. Error bars are 1 SD for total mean density. Means without shared letters differ at $p < 0.05$ for total density.

DISCUSSION

Although this assessment of an existing disturbance and an unreplicated operational management activity supported only limited statistical inference, our findings represent a case study of succession after land clearing in the eastern Mojave Desert, and how a particular set of restoration treatments may influence succession. Effects of individual restoration treatments cannot be discerned in this study, but the set of treatments including surface raking, applying artificial desert varnish, and planting of shrubs, appeared to make shrub composition on the treated 1998 corridor converge with that of the control (Figure 4). Although our study was not designed to track survival of individual plants in the planting, we found that *Larrea tridentata* established on the treated 1998 corridor at a density 36% of that of the control. No *L. tridentata* established on the untreated 1998 corridor. Previous studies of *L. tridentata* outplanting have produced widely differing results, ranging from complete mortality (Graves et al. 1978) or < 2% survival (Brum et al. 1983), to > 90% survival (Wallace et al. 1980; Clary and Slayback 1984; Newton 2001). In our view, the restoration treatments also made the 1998 corridor appear more similar to surrounding *L. tridentata* communities, an important consideration on National Park Service lands (Figure 1). This visual blending resulted from the *L. tridentata* establishment and also probably from the artificial desert varnish. Potential ecological effects of this darkening varnish remain unclear, but it could result in warmer soil temperatures or other effects. One of the largest aesthetic differences between the treated and untreated 1998 corridor and the control was that the control contained desert pavement. Pavement can require millennia to form (Elvidge and Iverson 1983), and it is unclear whether the raking portion of the restoration suite had an effect or will have an effect on surface layers such as desert pavement.

The approximately 20 cm of upper soil was salvaged, stockpiled, and reapplied after blading on both the treated and untreated 1998 corridor. Although salvage operations add logistical challenges and expense to projects, ecological effects of soil salvage are not well known in the Mojave Desert and require further study. Soil salvage effects cannot be evaluated in this study of an operational project because this would have required areas on the 1998 corridor that were bladed but did not have soil replaced. The effects of soil salvage and replacement after disturbance may depend on several factors, such as soil type, depth of salvage, and length of time soil is stored (Bainbridge et al. 1998). Effects also hinge on whether or not nutrients and seed banks are diluted upon reapplication by mixing upper and lower soil layers (Nelson and Chew 1977). Based on soil seed bank sampling in the northern Mojave Desert, Guo et al. (1998) reported that 91% of the total seeds were in the upper 2 cm of soil and only 9% occurred from 2-10 cm. Using these data and assuming that the 20 cm of salvaged soil in our study was evenly mixed during salvage operations, the upper 2 cm (likely the germination zone) of the salvaged soil would contain only 10% of the original seeds. Further reductions in viable seeds may occur during topsoil handling or storage. However, it is possible that soil salvage could result in nutrient retention. For example, Rundel and Gibson (1996) reported that total N below shrubs in the northern Mojave Desert was approximately two or more times more concentrated in the upper 5-9 cm of soil than in deeper layers.

Shrub species composition on the 38-year-old 1968 corridor is largely consistent with Vasek's (1983) classification of the successional status of species on an abandoned borrow pit in the Sacramento Mountains in the southeastern Mojave Desert. Three (*Stephanomeria pauciflora*, *Hymenoclea salsola*, and *Encelia farinosa*) of the five shrub species on plots within the 1968 corridor in our study were classified as "pioneer

perennials" by Vasek (1983). A fourth species, *Ambrosia dumosa*, was classified by Vasek (1983) as a long-lived opportunistic species that can be both an early and late-successional species. The last species, *Bebbia juncea* (Benth.) Greene, was not abundant in Vasek's (1983) study and was the least abundant of the five shrub colonizers of the 1968 corridor in our study. *Bebbia juncea* also was uncommon in a study of abandoned roads in Lake Mead National Recreation Area (Bolling and Walker 2000) and in a study of abandoned military camps in the eastern Mojave Desert (Prose et al. 1987). This species does appear capable of colonizing disturbed areas at low densities, however. Also similar to Vasek's (1983) classification, *Larrea tridentata*, categorized as a late-successional, long-lived perennial, was uncommon even after 38 years on the 1968 corridor.

Our findings on both the 1968 and the 1998 corridors concur with the long time scales reported in the literature for Mojave Desert plant succession (Lovich and Bainbridge 1999). For example, Webb and Wilshire (1980) found that perennial species composition on dirt roads abandoned 51 years previously still sharply differed from adjacent control areas at the Wahmonie ghost town site in the northern Mojave Desert. However, these early successional shrub communities are not necessarily "bad," depending on ecological management objectives. In fact, in our study, plant species richness in early successional shrub communities on the 1968 corridor was similar to the control, and exotic richness was actually lower (Figure 2). Plant assemblages similar to those on this corridor also characterize natural washes in this region (Wells 1961). Based on minimal colonization on the untreated 1998 corridor, however, these shrub communities take more than eight years to develop under the climatic and site conditions characterizing our study. It is possible that the direct planting of *Larrea tridentata* seedlings on the treated corridor bypassed the development of an early successional shrub stage. The planting allowed the late-succesional *L. tridentata* to circumvent high-mortality germination and early seedling phases that make natural regeneration an infrequent event (Barbour 1968).

ACKNOWLEDGEMENTS

LITERATURE CITED

Bainbridge, D., R. MacAller, M. Fidelibus, A.C. Newton, A.C. Williams, L. Lippitt, and R. Franson. 1998. *A beginner's guide to desert restoration*. 2nd edition. U.S. Department of the Interior, National Park Service. 35 pp.

Baldwin, B.G., S. Boyd, B.J. Ertter, R.W. Patterson, T.J. Rosatti, and D.H. Wilken (eds.). 2002. *The Jepson desert manual: vascular plants of southeastern California*. University of California Press, Berkeley, CA. 624 pp.

Barbour, M.G. 1968. Germination requirements of the desert shrub *Larrea divaricata*. *Ecology* 49:915-923.

Bolling, J.D., and L.R. Walker. 2000. Plant and soil recovery along a series of abandoned desert roads. *Journal of Arid Environments* 46:1-24.

Brum, G.D., R.S. Boyd, and S.M. Carter. 1983. Recovery rates and rehabilitation of powerline corridors. In *Environmental effects of off-road vehicles*, eds. R.H. Webb and H.G. Wilshire, 303-314. Springer-Verlag, New York.

Carpenter, D.E., M.G. Barbour, and C.J. Bahre. 1986. Old field succession in Mojave desert scrub. *Madroño* 33:111-122.

Clary, R.F., and R.D. Slayback. 1984. Revegetation in the Mojave Desert using native woody plants. In *Proceedings of the native plant revegetation symposium*, eds. J.P. Rieger and B.A. Steele, 42-47. California Native Plant Society, San Diego, CA.

Elvidge, C.D., and R.M. Iverson. 1983. Regeneration of desert pavement and varnish. Pp. 225-243 in *Environmental effects of off-road vehicles*, eds. R.H. Webb and H.G. Wilshire, 225-243. Springer-Verlag, New York.

Graves, W.L., B.L. Kay, and W.A. Williams. 1978. Revegetation of disturbed sites in the Mojave Desert with native shrubs. *California Agriculture* 32:4-5.

Guo, Q., P.W. Rundel, and D.W. Goodall. 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. *Journal of Arid Environments* 38:465-478.

Hunter, R., F.B. Turner, R.G. Lindberg, and K.B. Hunter. 1987. Effects of land clearing on bordering winter annual populations in the Mohave Desert. *Great Basin Naturalist* 47:234-238.

Kemp, P.R., and M.L. Brooks. 1998. Exotic species of California deserts. *Fremontia* 26:30-34.

Lathrop, E.W., and E.F. Archbold. 1980. Plant responses to utility right of way construction in the Mojave Desert. *Environmental Management* 4:215-226.

Lato, L.J. 2006. *Soil survey of Clark County area, Nevada*. U.S. Department of Agriculture, Natural Resources Conservation Service. 1801 pp.

Lovich, J.E., and D. Bainbridge. 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. *Environmental Management* 24:309-326.

Moore, C.B., and C. Elvidge. 1982. Desert varnish. In *Reference handbook on the deserts of North America*, ed. G.L. Bender, 527-536. Greenwood Press, Westport, CT.

Nelson, J.F., and R.M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. *American Midland Naturalist* 97:300-320.

Newton, A.C. 2001. DRiWATER: an alternative to hand-watering transplants in a desert environment (Nevada). *Ecological Restoration* 19:259-260.

Prose, D.V., S.K. Metzger, and H.G. Wilshire. 1987. Effects of substrate disturbance on secondary plant succession: Mojave Desert, California. *Journal of Applied Ecology* 24:305-313.

Rundel, P.W., and A.C. Gibson. 1996. *Ecological communities and processes in a Mojave Desert ecosystem: Rock Valley, Nevada*. Cambridge University Press, New York. 369 pp.

SAS Institute. 2004. *JMP user's guide*. SAS Institute, Inc., Cary, NC. 402 pp.

Vasek, F.C. 1979/80. Early successional stages in Mojave Desert scrub vegetation. *Israel Journal of Botany* 28:133-148.

Vasek, F.C. 1983. Plant succession in the Mojave Desert. *Crossosoma* 9:1-23.

Wallace, A., E.M. Romney, and R.B. Hunter. 1980. The challenge of a desert: revegetation of disturbed desert lands. *Great Basin Naturalist Memoirs* 4:216-225.

Webb, R.H., and H.G. Wilshire. 1980. Recovery of soils and vegetation in a Mojave Desert ghost town, Nevada, U.S.A. *Journal of Arid Environments* 3:291-303.

Webb, R.H., J.W. Steiger, and R.M. Turner. 1987. Dynamics of Mojave Desert assemblages in the Panamint Mountains, California. *Ecology* 68:478-490.

Wells, P.V. 1961. Succession in desert vegetation on streets of a Nevada ghost town. *Science* 134:670-671.

NOTEWORTHY COLLECTIONS
New Records of Lichen and Lichenicolous Fungi from California

ARTHONIA VARIANS (Davies) Nyl., San Diego County: Cuyamaca Mountains, Cuyamaca State Park, Fire Lookout Road, top of Cuyamaca Peak, 32° 56' 55" N 116° 36' 18" W, 1949 m, on apothecia of *Lecanora rupicola* on large granite boulders, 10 Oct. 2007, Knudsen 9138 (UCR).
Previous knowledge. Arthonia varians, a lichenicolous fungus, has been previously reported from North America from Arizona (Gila, Santa Cruz, and Coconino Counties) and Baja California (Guadalupe Island) (as *Arthonia glaucomaria* (Nyl.) Nyl., a synonym, Triebel et al. 1991; Grube 2007). *Opegrapha glaucomaria* (Nyl.) Källsten ex Hafellner also occurs on *Lecanora rupicola* and has not yet been reported from California (Ertz & Egea 2007). The ascospores of the two species are similar but easily distinguished: *A. varians* is characterized by ascospores 3–septate, usually constricted at septa, narrowly obovate, 13–18 x 4–7 μm, persistently hyaline (Grube 2007), while ascospores of *O. glaucomaria* are ovoid-oblong, sometimes ellipsoid or clavate, straight, hyaline, 3–4–septate, not or slightly constricted at the septa, larger, 18–26(–29) x 6.5–9 μm, and becoming dark when mature (Ertz & Egea 2007).
Significance. Arthonia varians is reported new to California, and is expected to be frequent. The host *Lecanora rupicola* and the related host *L. bicinta* are common lichens in montane habitats, esp. above 1500 m. *Opegrapha glaucomaria* is also expected.

BACIDIA BAGLIETTOANA (A. Massal. & De Not. ex A. Massal.) Jatta. Santa Barbara County: Santa Rosa Island, Channel Islands National Park, near Smith Highway between Lobo and Cow Canyons, 34° 0' 18" N 120° 5' 30" W, 150 m, on uplifted slabs of the Beecher Bay formation with *Niebla homalea,* 16 Oct 2006, Knudsen 7545.1 w/ Sara Baguskus (UCR).
Previous knowledge. Bacidia bagliettoana is a crustose lichen with a granular thallus and usually black apothecia, with a blue-green epihymenium, hyaline ascospores with 3 to 9 septa, 33–56 x 2–3 μm, and an orange-brown hypothecium. It occurs on bryophytes, decaying vegetation, plant debris, decaying lichens and calcareous soil, as well as occasionally on the bark of tree bases covered with bryophytes. It is known from Africa, Europe, North America, and New Zealand (Ekman 2004). It is locally common in eastern North America (*pers. comm.*, J.C. Lendemer, NY).
Significance. Bacidia bagliettoana is reported new for California and Channel Islands National Park on outcrops of the Beecher Formation. In western North America it has been reported as infrequent in the mountains of Arizona (Ekman 2004).

BUELLIA SCHAERERI De Not. San Diego County: Point Loma Ecological Reserve, on Navy land near water treatment plant on hillside, 32° 41' 0" N, 117° 14' 51" W, 51 m, on *Euphorbia misera*, 25 Jan. 2006, Knudsen 4984 w/ Andrea Compton (UCR); Point Loma, Cabrillo National Monument, coastal slope above second parking lot on Gatchell Road, 32° 40' 13" N, 117° 14' 23" W, 128 m, on *Euphorbia misera*, 15 May 2007, Knudsen 8427.1 (UCR).
Previous knowledge. Buellia schaereri is a widespread lichen species on bark and occasionally on wood, but is either rare or infrequently collected. It has small ascomata 0.2-0.4 mm with dark one-septate ascospores, mostly 7-9 x 3-4.5 μm (Bungartz et al. 2007). The ascospores are not constricted at the septum and have a narrow septum not thickening during spore ontogeny.
Significance. Buellia schaereri is reported new for California. It is expected to be frequent and under-collected or mis-identified as *Buellia punctata*..

Note: The first author (K.K.) collected extensively off *Euphorbia misera,* cutting branches for specimens with pruning shears. He got small amounts of sap on his hands. This was transferred to his eyes after sap dried causing drying out tear ducts then corrosive action on eye surface and severe pain. He ended up in emergency and had to have eyes flushed. He was fine by next day and his eyes had no permanent damage.

ENDOCOCCUS INCRASSATUS Etayo & Bruess. San Diego County: Henderson Canyon, Anza Borrego State Park, north-facing slope, 33° 18' 35" N, 116° 25' 21" W, 427 m, on *Placidiopsis cinerascens* on soil over granite, March 15, 2008, Knudsen 9538 w/ Tom Chester & Wayne P. Armstrong (PRM , UCR).
Previous knowledge. Endococcus incrassatus, a lichenicolous fungus, was only known from its type locality on the lower slopes of Cerro los Enjambress ca. 2 km WNW of Laguna Chapala in Baja California (Etayo & Breuss 2001). The species is distinguished by the superficial ascomata with thickening around the ostiole and dark one-septate ascospores 10.5-14 x 6-8 µm as well as its host, *Placidiopsis cinerascens.*
Significance. Endococcus incrassatus is reported new to California and the continental United States. This represents only the second collection of this species. The host *Placidiopsis cinerascens* is rare in California and *E. incrassatus* is also expected to be rare.

LICHENOSTIGMA RADICANS Calatayud & Barreno. Santa Barbara County: Santa Rosa Island, Channel Islands National Park, Lopez Road above Jolla Veija Canyon, 33° 54' 55" N, 120° 4' 40" W, 66 m, on *Aspicilia pacifica*, 15 Aug. 2007, Knudsen 8778.2 w/ Sarah Chaney & Silke Werth (UCR, PRM).
Previous knowledge. Lichenostigma radicans, a lichenicolous fungus, was previously known only from holotype collection from Spain on a vagrant *Aspicilia* (Calatayud & Barreno 2003).
Significance. Lichenostigma radicans is only the second known collection of this species and it is reported new to California and North America. The specimens match the original description as well as photographs of type. The determination of the host is tentative because ascospores were rare, conidia not found, stictic acid levels were low or non-existent, and only a small amount of norstictic acid was found in medulla. *Lichenostigma radicans* may be infrequent, nonetheless it can easily be overlooked and if ascomata are not ripe, impossible to determine.

LICHENOSTIGMA RUGOSUM Thor. Orange County: Santa Ana Mountains, Fremont Canyon, south ridge, above main truck trail, 33° 47' 24" N, 117° 41' 33" W, 490 m, locally abundant on *Diploschistes* species on decomposing sandstone slabs in shade above main truck trail, Dec. 3, 2007, Knudsen 9279 (PRM, UCR).
Previous knowledge. Lichenostigma rugosum belongs to the subgenus *Lichenostigma* with the ascomata not connected by superficial vegetative hyphae. The species is cosmopolitan in distribution and known from nine species of *Diploschistes*. It has been reported from the Middle East (Iran and Saudi Arabia), Australia, Europe, and North Africa. In North America it has been reported from Arizona, British Columbia, Colorado, Utah as well as Greenland (Alstrup and Cole 1998; Alstrup and Hawksworth 1990; Calatayud et al. 2004; Thor 1985 & 1995; Triebel et al. 1991). For detailed distribution see Kocourková (2000).
Significance. The species is reported new for California. It appears to be rare or infrequent in southern California, although it is a common lichenicolous fungus in other parts of its range such as the Czech Republic (Kocourková 2000).

Kerry Knudsen, *Lichen Curator, UCR Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, California 92521* *Knudsen@ucr.edu*
Jana Kocourková, *Lichen Curator, National Museum, Department of Mycology, Václavské nám. 68, 115 79 Praha 1, Czech Republic* *jana_kocourkova@nm.cz*

Acknowledgements

Cited Literature

Alstrup, V. and M.S. Cole. 1998. Lichenicolous fungi of British Columbia. *The Bryologist* 101(2):221–229.

Alstrup, V. and D.L. Hawksworth. 1990. The lichenicolous fungi of Greenland. *Meddelelser om Grønland, Bioscience* 31: 1–90.

Bungartz, F., A. Nordin, and A. Grube. 2007 (2008). *Buelllia.* In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 3*, eds. T.H. Nash III, C. Gries, and F. Bungartz, 113-179. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Calatayud, V. and E. Barreno. 2003. A new *Lichenostigma* on vagrant *Aspicilia* species. *Lichenologist* 35(4):279-285.

Calatayud, V., J. Hafellner, and P. Navarro-Rosinés. 2004. *Lichenostigma.* In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 2*, eds. T.H. Nash III., B.D. Ryan, P. Diederich, C. Gries, and F. Bungartz, 664–669. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Ekman, S. 2004. *Bacidia.* In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 2*, eds. T.H. Nash III., B.D. Ryan, P. Diederich, C. Gries, and F. Bungartz, 18-28. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Ertz, D. and J.M. Egea. 2007 (2008). *Opegrapha* In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 3*, eds. T.H. Nash III, C. Gries, and F. Bungartz, 255-266. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Etayo, J. and O. Breuss. 2001. *Endococcus incrassatus*, a new lichenicolous fungus (Dothideales). *Österreichische Zeitschrift für Pilzkunde* 10: 315-317.

Grube, M. 2007 (2008). *Arthonia* In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 3*, eds. T.H. Nash III, C. Gries, and F. Bungartz, 39-61. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Kocourková, J. 2000. Lichenicolous fungi of the Czech Republic (the first commented checklist). *Acta Musei Nationalis Pragae, Serie B, Historia Naturalis* (1999): 59–169.

Thor, G. 1985. A new species of *Lichenostigma*, a lichenicolous ascomycete. *Lichenologist* 17: 269–272.

Thor, G. 1995. Additional lichen records from Australia. 21. *Lichenostigma rugosa* Thor in Australia. *Australasian Lichenological Newsletter* 36: 20.

Triebel, D., G. Rambold, and T.H. Nash, III. 1991. On lichenicolous fungi from continental North America. *Mycotaxon* 42: 263–296.

BOOK REVIEWS

Introduction to the Geology of Southern California and its Native Plants by Clarence A. Hall, Jr. 2007. University of California Press, Berkeley, CA. 493 pp. $75.00.

UC Press has essentially cornered the market on massive treatises on the natural history of California. *Introduction to the Geology of Southern California and its Native Plants* is their latest hit, but it is more a ground-rule double than a homerun. When I first opened the book, I unconsciously expected it to be a Southern California version of Hall's classic *Natural History of the White-Inyo Range* (Hall was the editor and wrote the section on geology), but Hall's most recent contribution is a different kind of book and a very different read.

Introduction to the Geology of Southern California and its Native Plants includes an absolutely massive amount of information. There are 69 tables, 32 plates of color photos, and more than 70 figures. There are two glossaries, there are both a species and subject index, and there are more than 350 cited references. The book contains five sections and 21 chapters. It begins with a short overview, and then proceeds to a three-chapter section devoted to geologic concepts, a five-chapter section on geologic history in Southern California, a nine-chapter section covering the major geomorphic provinces, and then two chapters treating basic botany and the major Southern California plant families.

Although I originally anticipated that *Introduction to the Geology of Southern California and its Native Plants* might be a sort of geobotanical tour through Southern California, it never really succeeds in combining the two stated subjects, and personally I found the book somewhat schizophrenic. In this reviewer's opinion, *Introduction to the Geology of Southern California and its Native Plants* is chiefly valuable as a compendium of information on the geology of the southern half of the State. There is really only a smattering of interesting but disjointed botanical info, and the botany and plant family chapters are almost gratuitous. Many of the tables in the book are simply very long lists (some of these run 16-19 pages!) of selected plant taxa from different geomorphic provinces that Hall apparently assembled from different floras or from his field work. The lists do not include grasses or sedges (with one exception), and there is no information as to why certain species may have been selected for inclusion and others not. Indeed, it is not at all clear what purpose the lists serve.

If you want to know something about Southern California geology, you are likely to read about it in this book, *if you can find it!* Hall's book is confoundingly difficult to read (the syntax is awkward and complex and there are long digressions), confusingly organized, and – even with two glossaries! – undefined terms surface everywhere. For example, in the section devoted to a summary of the Ordovician Period in Southern California, Hall writes:

> "The *sequence* is composed of a relatively *conformable* succession of genetically related *strata* bounded at its top and base by unconformities or their *correlative conformities, stratal surfaces,* or *bedding planes.* The sequence boundary is an unconformity and correlative conformity marking a significant *basinward* shift in *facies* patterns. A *depositional sequence* is composed of sequence tracts. A sequence tract is a linkage of contemporaneous depositional systems. Each highland, lowland, or *transgressive* tract is defined by characteristic *parasequence stacking patterns* and each is interpreted to be associated with a specific part of the *eustatic* sea-level cycle. Parasequences are a relatively

> conformable succession of genetically related, *shoaling-upwards beds* bounded by marine-flooding surfaces and their correlative surfaces. These depositional sequences have a time-stratigraphic or *chronostratigraphic* significance in that all of the strata within a parasequence were deposited in a given broad interval of time." (italics mine)

None of the italicized terms in the above selection have entries in the glossaries (although, to be fair, some of them have a quick explanation of the term in parentheses hidden somewhere in the main text). The Introduction suggests the book is written for undergraduate-level students with no geology background, but there is some really dense stuff in here, and in this reviewer's humble opinion the layperson will find him/herself quickly lost.

Introduction to the Geology of Southern California and its Native Plants is apparently meant to serve both as library resource and field guide, although it is too big to easily carry in the field, and it simply isn't organized like a field guide ought to be. Typically, the geology of an area will be thoroughly (if confusingly) covered, then a very short paragraph will draw attention to a long list of plant species provided in an adjoining table. In a few cases some tidbits on plant ecology of an area are provided. I only found one road log-type entry, in the first chapter of the geomorphic provinces section ("Peninsular Ranges and Colorado Desert"), and it was confusingly done, with a very difficult map to understand. It almost appears as if the author intended to carry this through the other chapters, but ran out of time, patience, or interest.

In summary, *Introduction to the Geology of Southern California and its Native Plants* could have used a heavy dose of old-fashioned editing. Hall's intentions are admirable, and his book is a veritable bible of geological information, but as with the Bible itself, this book will require a translation to the vernacular before it becomes really useful to the common man.

Hugh D. Safford, *USDA-Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592, and Department of Environmental Science and Policy, University of California, 1 Shields Avenue, Davis, CA 95616. hughsafford@fs.fed.us.*

Become a Member of
Southern California Botanists
Today!

☐ Individual (family) $15.00   ☐   New Member

☐ Organization $25.00   ☐   Renewal

Name _____

Address 1 _____

Address 2 _____

City _____ State _____

Zip code _____ Phone (optional) _____

E-mail address _____

In addition, I would like to give $_____ to help support SCB.

Make checks payable to Southern California Botanists and mail to:

Alan P. Romspert
Department of Biology
California State University
Fullerton, CA 92834

Southern California Botanists, Inc.
— Founded 1927 —

Memberships, Subscriptions, and Back Issues

Individual and Family Memberships in SCB are $15 per calendar year domestic, and $20 per year to foreign addresses. Membership includes two issues of CROSSOSOMA, and 5 or 6 issues of *Leaflets*, the newsletter of SCB. *Leaflets* provides time-dated information on activities and events that may be of interest to our membership. A subscription to CROSSOSOMA is available to libraries and institutions at the domestic rate of $25 per calendar year, and $30 to foreign institutions. Back issues (Volumes 18-present) are available for $5 each, or $10 for the volume, postpaid. Prior to Volume 18, CROSSOSOMA included time-dated notices to the membership and was published six times a year. These back issues of Volumes 1-17 are $1 each, or $6 per volume, postpaid. Some back issues that are out of stock may be provided as photocopies.

Available SCB Special Publications

No. 1 A Flora of the Santa Rosa Plateau, by Earl W. Lathrop and Robert F. Thorne, 39 pp ……..……..……………………………...…………...………………………..…..$7.00

No. 3 Endangered Plant Communities of Southern California, Proceedings of the 15th Annual SCB Symposium, edited by Allan A. Schoenherr, 114 pp………………....$12.00

No. 4 Flora and Ecology of the Santa Monica Mountains, 194 pp………….……..$40.00

By request, the following article has been reprinted separately, with covers, and is available for plant collecting workshops:

> Herbarium specimens as documents: purposes and general collecting techniques, by T.S. Ross [from CROSSOSOMA 22(1):3-39, 1996] …….....…. $3.95 each; 10 for $22.50

Prices include California state sales tax, handling, and domestic postage.

Applications for membership, requests for purchases of Special Publications and back issues, name or address corrections, and requests for replacement of lost or damaged CROSSOSOMA issues should be sent to **Alan Romspert, Treasurer Southern California Botanists, Inc., Department of Biology, California State University, Fullerton, CA 92834, USA**. Consult the website for current email contact information. Make your check or money order payable to *Southern California Botanists*, or *SCB*.

http://socalbot.org

Southern California Botanists
Department of Biology
California State University
Fullerton, California 92834 U.S.A.